A STUDY OF SOME PHASES IN THE ECOLOGY OF *RANA SYLVATICA* LE CONTE

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BREEDING BEHAVIOR

Introduction

The woodfrog in the Itasca Park region selects breeding ponds usually characterized by the presence of sedges, Carex sp., or other emergent vegetation. The ponds most frequently utilized are wooded at least along 50 percent of their shoreline. Coniferous, deciduous or mixed woods surround these ponds. Coniferous species that may constitute these associations are: Abies balsamea, Larix laricina, Picea glauca, P. mariana, Pinus resinosa and P. strobus. The most common deciduous trees are: Acer rubrum, A. saccharinum, A. saccharum, A. spicatum, Alnus rugosa, Fraxinus pensylvanica, F. nigra, Populus tremuloides, Quercus borealis and Q. macrocarpa. Mixed conifer-deciduous associations resulting from early logging operations are common.

Most of the breeding ponds are temporary and many of them are fed by runoff following substantial rainfall. Others appear to be remnants of bogs that are in the normal successional process of filling in; these are often spring fed.

Methods of Observation

Because the breeding behavior of the woodfrog is

dependent upon ambient temperatures, most observations were made in the afternoon after the ponds had warmed. It was only after a fair-sized chorus (25 or more frogs) was established that any observation could be made. Males in small groups seemed to be extremely wary, dived at the slightest disturbance and remained out of sight for lengthy periods of time. Attempts to observe such small choruses were simply not feasible in terms of time expended. Consequently, most detailed observations were made from about 1600 to 2000.

Lengths of observational periods varied with the physical dexterity and chillability of the observer. There were two methods used to approach a chorus. If the chorus was well established and large, an aggressive, fairly swift walk into the area could be made. When small, a very slow sneak was in order. In either case, often the chorus members abruptly ceased calling and dived, remaining under water and surfacing later to rest on the surface. Vigorous choruses would usually commence their normal activity almost immediately and usually took no longer than five minutes. It was not unusual to wait as long as 30 minutes for a less vigorous chorus to resume normal activity. During this time any movement by the observer caused all frogs to dive.

After the chorus had become re-established, it

was possible to shift one's stance and body posture if it was done slowly. Undisciplined movements again brought momentary halts to the activities.

It was possible to approach to within less than five feet of the egg deposition sites. Once the chorus members became accustomed to the observer there seemed to be no obvious effects on behavior. In fact, I have had frogs in the chorus rest their forelegs on the legs of my waders and call.

Results

General Behavior

Breeding behavior in Rana sylvatica can be described as brief, noisy and social. The woodfrog is one of the earliest breeders in Minnesota, the earliest of the ranid frogs and preceded perhaps only by the chorus frog, Pseudacris nigrita, among all anurans in the state.

In 1966, Itasca woodfrog males began calling on April 25. A high of 45°F was reached during the day. On April 26 a trip was made to the park; the temperature reached a high of 42°F. During the trip snow had started to fall and upon arrival at the Itasca Biological Station about three inches of snow lay on the ground.

Arrival time was approximately 2300 and upon learning from Mr. Robert Fladung that the choruses had been very active during the day, it was decided to check Icehouse Pond, a small pond close to the station, for woodfrogs. A reconnaissance of the pond revealed no frogs although a single weak call was heard.

Snow continued to fall throughout the night of the 26th, accumulating to six inches. A check of several ponds in the morning was disappointing since no amphibians were heard calling. The weather forcast and a threatening sky convinced my advisor and me that a return trip to Minneapolis was advisable. This action proved to be very fortuitous since six additional inches of snow fell. The high temperature

on the 27th was 34°F. The high temperature was 35° F through April 30 and the low averaged 20°F. A return trip to the park was made on the evening of the 5th of May, 1966, by which time the frogs had resumed breeding activity. On May 6 in Bert's Pond South (Figure 1) at 1730 the following observations were made; they were recorded while standing five feet from the ovipository site. This spot was located approximately five yards from the west end of the pond at the base of a clump of willows. There were three woodfrog egg masses and a single chorus frog's egg mass among them attached to the previous year's sedges. The R. sylvatica masses were resting about 1/2 to 1-1/2 inches below the water's surface.

In the immediate area were two amplexing pairs and several single males. One of the mated pairs approached the egg masses and clung to them through a grasping action by the female. Periodically they would move away from the masses and then return. All movements took place at the water's surface with the female providing the major propelling force. The male participated in the swimming movements, however his efforts appeared subsidiary.

A single male attempted amplexus with both mated pairs and in both instances was unsuccessful. The mated males emitted a warning cry upon being the object of an amplexus attempt. During these encounters the calls

were effective in preventing further pursuit by the unmated males. Attempts at amplexus by other male frogs were met by vigorous kicks, sometimes coming from the male member alone and at other times from both members of the pair.

Pre-oviposition behavior consisted of the female's submergence carrying the pair below the surface of the water. Once beneath the surface she positioned herself with her head pointing down and grasped a sedge blade with her forearms. She then paddled and stroked the sedges with her hind feet. While this behavior was exhibited by the female the male allowed his legs to float freely. Each leg formed a 90 degree angle between the femur and tibia-fibula.

Oviposition is signaled by the male who flexes his hind legs, drawing them close to his body and in doing so, brings his cloaca in apposition to that of the female. As the eggs are extruded the male pushes them away with his hind feet. Following egg deposition by the female two sperm ejaculations were seen to occur in rapid succession. Whether any sperm were emitted during the egg laying was not established. The entire process lasted for two minutes.

The pair remained in amplexus for three minutes following oviposition, whereupon the male released his grasp, surfaced, remained on the surface for approximately one minute and swam away. He successfully

warded off an amplexus attempt by another male. After clasping the sedge for two minutes following release by the male and after disengaging herself from the egg mass though a series of "scratching" movements, the female dived toward the bottom of the pond. It was impossible to follow her actions further since she scrambled under the dense bottom cover of dead sedges.

The fresh egg mass was very compact, approximately 1/4 to 1/3 the size of the older masses or about 1-1/2 inches in diameter; this was due to the unswollen condition of the jelly coats.

Male Breeding Behavior

Male breeding behavior begins with the establishment of a chorus as is characteristic of most anurans. Chorus development has been observed several times, however never from the first frog's initial call.

On May 6, 1966 in Bert's Pond South (Figure 1) the initial chorus at the west end numbered about a dozen animals by sight count. Males when approaching the breeding area used two different methods of advancing toward the chorus. They swam underwater for distances of four to six feet, surfaced, called, submerged, swam beneath the surface and continued in this way until the general vicinity of the egg mass was reached. The more common method of approach was to swim on the surface, paddle with the hind feet, and call while resting at

the surface with about 1/3 of the body protruding. In this position the hind legs floated close to the surface and were spread so that the tibia-fibula made an obtuse angle with the thigh.

The latter resting position was used when the chorus had become well established, hence of a large size, and the individuals were in proximity so that extended investigative movements and the underwater swimming were not necessary in order to reach other individuals. Males, upon reaching the periphery of such choruses, were immediately the objects of attempted amplexus and initiated other encounters themselves.

Another resting position was observed in both sexes throughout the study period. The animal clung to the vegetation with its head protruding out of the water to just posterior to the eyes. The body and hind limbs formed an acute angle with the water's surface.

Males exhibit two different behavior patterns after joining a chorus: (1) stationary behavior, (2) searching behavior. The stationary behavior pattern can be further subdivided with regard to call frequency: (1a) The male was quiet while resting on the surface in the spread-eagle position described above, (1b) the male remained stationary while emitting single calls or a series of calls up to three in number. Very rarely did a frog move during a series as short as this nor were longer call series associated with the stationary

behavior pattern. Searching behavior is accompanied by a series of calls as many as nine or more and almost always greater than three. Investigative movements are directed toward surface disturbances, especially those movements made by other members of the chorus. On occasions woodfrogs were seen to investigate Pseudacris, the chorus frog, that surfaced among the woodfrog chorus members. Other than warning calls, to be discussed, a single (mated) male frog has only once been heard to utter the mating call and this was simply a single call.

The vocal sacs during the breeding season are very evident even when deflated. They appear as a pair of very pliable areas, rather reminiscent of partially filled water balloons about an inch in length. During a single call the sacs are inflated to about half their capacity. Full inflation occurs only during a series of calls and makes the frog appear as though it had a set of waterwings. The sacs remain inflated during flurries of activity accompanied by repeated calls. When calls are intermittent the sacs become flaccid between calls.

Behavior of the males toward each other may take several forms. One of these, the most vigorous observed, was an attempted axillary amplexus during which the male being clasped struggled violently and uttered a rapid series of low-pitched, rasping notes,

the "get-off-my-back" call. The recipient male may merely struggle, however and remain mute.

In some instances males were seen to place one front leg around another male and quickly withdraw the limb with hardly enough time to evoke a response from the other male.

Many times a male would rush over to another male and butt him with the snout tip at about the angle of the jaw but no attempt at amplexus was seen after these encounters. Butting may occur repeatedly between individuals.

Apparently a further deterrant to amplexus attempts is recognition of the call. Males were observed to swim rapidly toward another male; if the frog being approached called, the "agressor" turned and swam away. An alternative explanation may be that the frog was recognized as a male because of the distinctive non-female profile presented by the inflated vocal sacs.

Male/Female Behavior

Heterosexual relationships observed were somewhat less vigorous. A male was seen to attempt amplexus with a female who resisted. He left her to investigate another frog by which he was rejected and returned to successfully amplex with the first female, which did not resist the second attempt.

During two other successful pairings the females

were grasped by the males and offered no resistance. In one case the male moved around until he apparently secured a better grip. Once the male established a firm hold the female dived. Similar behavior was displayed by both females following amplexus.

Oviposition Sites and Egg Masses

Sites chosen for oviposition are often located at the base of trees or shrubs (willow or alder). Recently flooded trees or shrubs are not selected because of the lack of appropriate vegetation for egg mass attachment at their bases. Usually the eggs are attached to the previous year's sedge leaves.

Due to the behavioral habit of deposition of masses at a common site the discovery of their location becomes tedious, especially if the pond is of any size or has many flooded shrubs or trees. Egg masses at these places number 50 to 100 per site with more than 200 having been estimated in Icehouse Pond in 1966 and in 1967. Single masses observed were often in proximity to a large group of masses. Water depths at the sites did not exceed 12 to 24 inches of water.

In a sample of 19 egg masses taken from Long Pond on April 28 and May 5, 1967, the average number of eggs per individual mass was 863 (SE = 47) eggs. The range was 556-1180 eggs.

On two occasions examples of group amplexus were

observed. This behavior was noticed when a considerable disturbance became evident at the surface of Long Pond. The chorus at the time was well developed with perhaps 200 to 300 males in the group. In the immediate vicinity of the disturbance were about eight frogs which appeared to be engaged in frenzied searching and amplexus attempts.

Upon investigation the disturbance proved to be caused by a group of five frogs, four males and a single female. One male was clasping the female immediately anterior to the hind legs while another had one arm around a male and the other in the female's chest region. The two others were attached to the group haphazardly. When they were separated, the members of the group dived.

Another instance of multiple amplexus could not be investigated because the members voluntarily dispersed upon my approach.

Discussion

It is quite probable that the woodfrog's breeding will be interrupted in northern Minnesota by adverse weather. In the three years that observations were made, 1965 through 1967, only during 1965 was breeding explosive with choruses present in all available ponds (James C. Underhill, personal communication). In 1966, frogs began chorusing on April 25 and their breeding

activities were suspended until May 3 by snow and cold weather. Choruses began again in 1967 on April 25 and again cold weather made breeding very spotty with eggs being deposited during warm days and nights. This sort of breeding behavior would be advantageous to a frog having a distribution such as the woodfrog. The ability to resume breeding during intermittent warm spells coupled with rapid embryological development at low temperatures (Moore 1939) probably were responsible for the woodfrog's extension of its range to the Arctic Circle.

Selection of egg deposition sites is problematical. Eggs were found grouped near pond margins in all directions of the compass and almost always attached to sedges or grasses. In Long Pond in 1966 and 1967 there was a single site of egg deposition at the northeastern end. Trees or bushes appear to be attractive and very often they become deposition sites. Since the female directs the movement of the mated pair, it may be she that chooses the actual site. However, the male choruses are clustered primarily in the vicinity of these sites, which perhaps makes the choice of site actually the responsibility of both sexes.

Perhaps the placement of eggs beneath shrubs and at the bases of trees is an adaptation for protection from predators. Air-borne predators, in particular, would be deterred by such placement. Little is

known concerning predation of anuran eggs. Savage (1961) states that Moorhens, Gallinula chloropus, sometimes eat the eggs of R. temporaria, a European frog closely related to R. sylvatica. R. temporaria does not attach its eggs to vegetation nor does it frequent bushes as deposition sites.

Although mated pairs would appear to be susceptible to amplexus attempts and indeed they seem to be "tried" by any available male, pairs are quite effective in warding off other males. Both physical and vocal deterrants are utilized. Often one sees pairs resting near the pond edge indicating that some females may be captured as soon as they enter the pond. Such pairs must then make their way to the laying site, which would expose them to numerous encounters with unpaired males unless the approach were made submerged.

The approaches seen in males during chorus formation are most likely related to the maturity of the chorus. During the first stages of formation when very few frogs constitute the group and animals may be coming from long distances, the underwater approach is most common. When the chorus has grown to some size, the distance required to join it has decreased so that frogs approaching will be testing the chorus members and therefore travel in short spurts on the surface.

Banta (1917) reported that males moved on the surface and females used the underwater approach. My observations indicate that both approach methods are used by males. Furthermore, in the several hours spent observing mating of woodfrogs I never observed a female's approach. In all probability this is due to the fact that the sexes are indistinguishable and Banta may have confused males using an underwater approach with females.

Male frogs' actions upon joining the chorus are dependent upon the size and vociferousness of the chorus. Quiet resting is most often seen in small choruses, as one might expect, since reactions among members are fewer than in a large group. Resting, accompanied by a series of 1-3 calls, is alternated with the extended frantic movement accompanied by a series of 3 or more calls. In small choruses the intensive searching and calling seems to be generated in waves. One member starts the movement followed by the rest of the chorus, then there is a period of quiet resting, possibly accompanied by single calls, then the concerted searching begins again. Chorus members of large groups are frantically searching and calling most of the time. Banta (1917) also observed these three different behavior patterns upon chorus arrival.

Banta (1917) and Noble and Farris (1929) have

discussed the role of various aspects of behavior in sex recognition in Rana sylvatica. Banta suggested that possibly color and the differential movement behavior (males at the surface and females underwater) were involved as well as possible chemical stimulation. Noble and Farris took exception to Banta and following a series of experiments concluded that girth differences were the primary recognition factor.

I feel that several factors may be involved. The difference between male and female girths may be important in recognition; however, there are other signals recognized by males that reinforce discrimination. The fact that male/male amplexus attempts are met by vigorous resistance often accompanied by the warning cry may be equally important. The warning call is very distinctive, being lower pitched than the mating call, and it can be heard at all seasons of the year when males come into contact with one another. The near approach of individuals without bodily contact suggests a recognition factor that is probably not girth difference, acting at a distance. Possibly some frogs are able to perceive a difference in profile. Often a distant recognition follows a call by the stalked individual. Inflation of the vocal sacs may provide a distinct profile. Head butting by males undoubtedly serves as a male/male recognition signal since amplexus attempts never followed.

Of the few instances of successful amplexus observed, only one was preceded by a vigorous rejection by the female. The others were swift, brief and successful. Banta (1917) reported that the females were extremely vigorous in their attempts to evade the males. My observations do not substantiate Banta's generalization.

The paddling and stroking of the sedge by the female prior to oviposition is probably similar to the backward shuffling described for Rana pipiens by Noble and Aronson (1942) and it may be similar to the ill-defined "scrambling movements" described by Savage (1961) for Rana temporaria. Noble and Aronson reported a series of shuffling, resting, and swimming followed by shuffling movements in R. pipiens. The only shuffling noted in the woodfrog occurred immediately prior to egg deposition and probably was the beginning of the mating posture.

A difference seen between the two species was the male's leg posture. The male R. pipiens kept his legs flexed during amplexus (Noble and Aronson 1942) whereas the male woodfrog allowed his legs to float free during the pre-ovipository period. Just prior to oviposition the male woodfrog flexes his legs thereby bringing the amplexed pair's cloacae in close apposition. Perhaps the kicking movements that the male exhibited during the egg laying were what Noble and Aronson (1942)

described as ejaculatory pumps. No sperm emissions were seen during these kicks. In fact, the two sperm emissions witnessed were not accompanied by kicks.

Female woodfrog leg position was not altered prior to oviposition as it was with R. pipiens (Noble and Aronson 1942). The legs appeared to remain in the typical resting position.

The time taken by the woodfrog for spawning was half that recorded for natural oviposition in R. pipiens by Noble and Aronson (1942). Savage (1961) recorded an egg deposition duration of about five seconds for R. temporaria. His observations were made of frogs taken during the breeding season and placed in aquaria. The observations recorded for R. pipiens were made on animals collected during September through April. These frogs were then injected with pituitaries that induced ovulation in the females and produced sexually excited males. Under these conditions, perhaps the time element was prolonged. Oviposition time for R. clamitans ranged from 10 to 25 minutes with observations made on pairs whose female members had received pituitary injections (Aronson 1943). Apparently there is considerable interspecific variation in the duration of oviposition time.

Perhaps the duration of the ovipository period is related to the egg deposition behavior exhibited by

the different species. In R. sylvatica and R. temporaria (Savage 1961), which are submerged during deposition and in R. pipiens, which is sometimes submerged (Noble and Aronson 1942) the time is short, five seconds to four minutes. Rana clamitans deposits eggs as a surface film during which the male has his head above water (Aronson 1943), the spawning time is longer (10 to 25 minutes). Toads, which spawn with both members above water, have very long ovipository periods, three to more than five hours (Aronson 1944). The ovipository period may be the most vulnerable portion of the reproductive cycle and those that spawn underwater are probably the most vulnerable to predation due to their limited vision underwater. The swift oviposition may have arisen as an adaptation to the selection pressure of predator vulnerability.

Multiple amplexi are occasional phenomena seen during the height of the breeding season and were reported by Banta (1917) and in R. temporaria (Savage 1961). Probably only among sizable breeding congresses of several hundred do these occur. In small groups the breeding fervor does not attain the intense heights that it does in the larger groups, hence the probability of the occurrence of a group amplexus is lower. Proximity of individuals is also a contributory factor. The formation of the groups may be due to a faulty initial single pair amplexus. The male, for

example, may gain a waist hold rather than the normal axillary grip. Such a hold would allow other males access to the female and the resulting agitation might act as a stimulus to the closely spaced males. When a third frog succeeds in gaining a hold on a pair an awkward situation prevails which caused a greater commotion, etc. Apparently, however a mated pair's defensive kicking and the male's warning call are normally quite efficient in warding off extra males, since the multiples are rare.

TADPOLE GROWTH

Introduction

Tadpole growth studies have been made primarily on laboratory reared animals and many observations of maximum sizes of various anuran larvae can be found in the literature. Recently a study of the growth of Alaskan woodfrog larvae was conducted by Herreid and Kinney (1967). Part of their study was concerned with total length and weight of animals in three ponds during the summer of 1965.

Adolph (1931) studied animals taken from a wild population of Rana pipiens using body weights to construct growth curves. The tadpoles were laboratory reared. Etkin's paper (1932) described growth and the events of metamorphosis in R. palustris, R. clamitans, and R. catesbeiana. The latter study was based on laboratory animals also.

Studies of wild R. temporaria larvae in Great Britian by Savage (1961) revealed that the tadpoles of this species congregate in what the author called colonies. Each of the colonies exhibited its own distinct growth rate.

The present study was designed to compare growth rates of body proportions and weights between the

populations of Rana sylvatica tadpoles from two ponds which were very different in their environmental surroundings and physical features. Temperature influence on tadpole growth during the study was analyzed.

There have been no extensive attempts to compare body measurements of tadpoles to provide criteria for identification and characterization of anuran larvae. Wright and Wright (1949) include some ratios; however, the individual species ranges are rather broad, and there are species overlaps and therefore these ratios are not particularly useful. Some of the ratios discovered in animals prior to metamorphosis may aid in characterizing the woodfrog tadpole by use of body measurements.

Some studies (Bresler and Bragg 1954; Gosner and Black 1954; Bragg and Hayes 1963) have shown that tooth rows, which are used extensively for identification of larvae, are variable and tend to increase in number with ontogeny. Tooth row variability has never been studied in any detail for a ranid frog, although Orton (1952) states that R. sylvatica tadpoles exhibit some variation. The tooth row variation was examined in some detail during the present study. Samples were compared to discover whether tooth row number bore any relation to ontogeny or size. Since larvae of other anuran species appeared to add tooth rows with age it

was suspected that R. sylvatica might also.

Observations on behavior were made during the course of the study and are included in the results.

Materials and Methods

Collections of larvae were made using a dip net constructed of galvanized screening attached to a four foot wood handle by means of an aluminum clamp. This sampling technique was necessary because of the heavy growth of vegetation in the ponds; no other method was feasible. Consequently, collecting periods tended to be long since captures usually consisted of single individuals. Cloud cover presented yet another problem because the larvae were more difficult to see.

Captured tadpoles were placed in glass gallon jars containing pond water and transported back to the Itasca Biological Station where they were stored in a refrigerator at 5° C until they could be examined. Larvae were usually processed the following day and no more than three days elapsed between collection and scoring of the animals.

To facilitate measurement, each tadpole was placed on a grooved slab of lucite which rested on the glass stage of an Elgeet binocular microscope. The grooved plastic held the animal in a maneuverable position, yet allowed suitable illumination. The

following measurements were made with a Helios micrometer calibrated to .1 mm:

1) total length - taken from the snout tip to the tail tip

2) standard length - taken from the snout tip to the posterior margin of the anal canal piece.

3) tail depth - measured at the deepest part of the tail fin.

4) body width - measured approximately midway between the posterior edge of the eyesocket and the anterior edge of the spiracle.

5) body depth - measured from a point between the eyes to a point on the ventral part of the body directly below the eyes.

6) interorbital space - measured between the medial edges of the eyesockets.

7) internaral space - measured between the medial edges of the nares.

8) hind limb bud measurements were made from the insertion of the thigh on the body to the end of the longest posterior protuberance or fourth toe of the right limb. As the larvae aged, their legs were held in the familiar flexed position of the frog at which time the measurements were divided into femur length, tibia-fibula length, and ankle-4th toe length which were then summed to obtain the hind limb length.

9) labial tooth row number - upper and lower row numbers as well as anomalies such as split rows were recorded.

10) wet weight - the animal was carefully rolled on a paper towel to remove as much external moisture as possible, transferred to a numbered, tared glass petri dish, and weighed on a Mettler balance to .01 g. The animal was then placed in an oven set at 105° C.

11) dry weight - after about seven days at the above temperature the tadpoles were removed from the oven, allowed to cool and weighed on the Mettler.

12) ash weight - the dried larvae were placed in a furnace set at 500° C for about one hour, cooled and weighed.

The tail length was calculated as the difference between the total length and the standard length. Additional information such as hind limb development; i.e., foot shape, toe development and pigmentation were noted; forelimb development and eruption were recorded.

The following terminology, originally proposed by Etkin (1932), is used concerning three phases in the tadpoles' life history: premetamorphic - the period during which the hind limbs were no more than 5 mm in length; prometamorphic - the period characterized by rapid hind leg growth; climax metamorphosis - the period commencing with the emergence of front legs.

Long Pond

Long Pond is approximately 100 yards long by 30 yards wide and is oriented on a northwest-southeast axis (Figure 8). It is located 3/8 of a mile north of the Itasca Park Biological Station.

The water depth is about 24 inches for 3/4 of the length of the pond. At the south end is a floating mat of debris and rotten sedges supports some small willows. The pond's depth at the edge of the mat is 3-1/2 to 4 feet and probably deeper below the mat. It appears that the pond is probably in the late stages of bog succession with a sedge mat having developed from the northwest and proceeded southeast leaving a hole at the south end.

At the northern end of the pond, sedges, Carex sp., are the sole emergent plant present. Near the "open" southern end at the margin of the mat were the emergent plants, sweet flag, Acorus calamus, and wild calla, Calla palustris.

Along the eastern margin of the pond are red pine, Pinus resinosa and quaking aspen, Populus tremuloides, with the red pine more numerous. The woods along the western side is primarily aspen. At the edge of the pond are alder, Alnus; serviceberry, Amelanchier; and willow, Salix.

Wood Pond

Wood Pond is a small temporary pond situated 1/4 mile south of the Itasca Park Biological Station and 1/8 mile southwest of the park drive. The pond is oriented on an east-west axis and is approximately 25 yards long and 7 yards wide and is the last of a series of ponds lying north of the east arm of Lake Itasca (Figure 9). The ponds act as holding basins for the drainage of the ridge paralleling LaSalle Trail, the ridge trends southwestward after crossing the park drive.

Water depth ranged from 12 inches to about 36-48 inches on the west end of the pond. Two old fallen logs were present in the pond. The log on the east end extended from the south margin almost to the north margin. Growing on this log were a luxuriant Sphagnum mat and three young fir saplings. The other log lay across the entire width of the west end and it too had a moss growth with an ash sapling growing on it. The portion of the pond west of this log was almost devoid of vegetation, probably due to the heavy shade. On the east side of this log was the deepest part of the pond that supported a thick growth of wild calla, Calla palustris. Also present around the deeper portion of the pond were water plantain, Alisma sp.; water parsnip, Suim suave; reed-meadow grass, Glyceria grandis; rattlesnake grass, G. canadensis; and sedges, Carex sp.

A very profuse sedge growth was present at the east end of the pond.

Alders, Alnus sp., are found around the margin of the east end of the pond and extended about half-way around the margin of the north side. Two alder clumps grew in the pond near the northern margin. Black ash, Fraxinus nigra, grew along most of the rest of the pond's margin. Also growing near the pond's margin were: bur oak, Quercus macrocarpa; American Elm, Ulmus americana; quaking aspen, Populus tremuloides; sugar maple, Acer saccharum; silver maple, A. saccharinum; moutain maple, A. spicatum; white pine, Pinus strobus; red pine, P. resinosa; balsam fir, Abies balsamea; and white spruce, Picea glauca.

Wood pond is situated in a mature spruce-fir stand; the north slope is almost a pure stand and the south slope is dominated by the two species, however also interspersed with aspen and paper birch, Betula papyrifera.

Pond Temperature Records

The two ponds chosen for the growth study were selected for their dissimilarities since the contrast between a small woodland pond and a large, less shaded pond might produce two populations of larvae with different growth rates.

Temperatures in the two ponds were monitored

during the period June 17 through July 4, through the use of a Model 1000 seven day recording thermometer made by the Electric Auto-Lite Company. The sensing probes were placed approximately 18 inches from the pond's margin in about 12 inches of water. They rested on the bottom of the ponds and were shaded by placing water-soaked leaves over them. As the water level dropped, the probes were repositioned to maintain the 12 inch depth relationship.

Striking differences were seen between the temperature records of the ponds (Figure 2). Average high and low temperatures were calculated for both ponds; all daily highs and lows were averaged separately. The mean high temperature for Long Pond was 71° F while that of Wood Pond was 63° F. A mean low temperature of 66 degrees was calculated for Long Pond, whereas that of Wood Pond was 47 degrees. Only a 5 degree difference existed during the study between the high and low temperature means of Long Pond indicating a rather stable temperature regime. Wood Pond mean temperatures during the study differed by 18 degrees.

A tabulation of diel fluctuations was made for each of the bodies of water. Degrees were summed for daily traces between 0000 hours (midnight) of one day to 0000 hours (midnight) of the following day. Daily totals were composed of the sums of degree changes with no regard to the temperature trend. Changes were

important, not the direction of change. On 12 of 16 days in Long Pond the recorder pen traced a line through a total of 9 degrees or less. On half (8) of these days the total was 4 to 5 degrees. In Wood Pond on 9 of 16 days the recorder traced a line through 14 to 29 degrees. On 7 days the trace traveled through 38 to 48 degrees.

The highest readings in both ponds occurred during a five day period beginning June 29 and ending July 4. The high temperature in both ponds exceeded 75° F and on June 30 a high of 81° F was recorded in Long Pond and 83° F in Wood Pond. During this time the high air temperatures at the Lake Itasca Biological Station ranged between 86 and 93° F. Earlier in the study, there was a three day period when the air temperature reached 86° F. Pond temperatures during this time did not exceed 70° F in Long Pond and 63° F in Wood Pond. Water levels in the ponds at the time of metamorphosis had dropped considerably, especially in Wood Pond. The latter pond was reduced to a pool 4 feet in diameter and about 30 inches deep located at the east end. The pool was heavily choked with live and rotting vegetation and debris. The reduction in water level undoubtedly influenced pond temperature.

Population Growth - Long and Wood Ponds

Growth of tadpoles in total length in both ponds

followed similar patterns (Figure 3). There was an increase in total length during the first four weeks of the study with the difference between weeks being statistically significant (Table 1a and 2a). Analyses of variance comparing samples taken from the two ponds revealed that only during the third week was the difference between the total lengths significant with Long Pond exhibiting the greater length (Table 3a).

Standard length growth curves within each pond were very similar (Figure 3). Both ponds exhibited nonsignificant differences in growth in some weeks during the course of the study (Table 1b and 2b). Comparisons made between ponds revealed no significant differences between ponds for week one and week two but there were significant differences during weeks three and four with tadpoles from Long Pond exhibiting the greater standard lengths (Table 3b).

Differences between tail lengths in the two ponds were not significant except during the third week (Table 3c). During the period between the third and fourth week a significant difference in tail length was seen in Wood Pond but no significant difference was observed in Long Pond.

Tail height growth of tadpoles from Long Pond was significantly different for all time periods (Table 1d). This was not true of Wood Pond animals (Table 2d). A comparison of weekly growth between

the ponds revealed that tail heights were significantly different between the populations only during the third week (Table 3d).

Interorbital and internaral distances (Figure 3) between the populations of the two ponds were significantly different during the third week only; tadpoles from Long Pond exhibited the greater measurements (Table 3e and f).

Ontogenetic Growth

Standard Length - Total Length Relationship

Standard length - total length ratios for larvae from Long Pond were comparable to those of tadpoles from Wood Pond (Table 4). The ratios remained very similar during the study prior to the onset of metamorphosis. Apparently the growth gradient along the long axis of the tadpole was homogeneous throughout ontogeny. It appears from these ratios that the growth of the larval body (standard length) and total length (standard length and tail length) was very nearly isometric.

Standard Length - Body Width

Apparently the relative growth rates of the tadpole's body both in length and width are very similar. Prior to climax metamorphosis stages the ratio between these two dimensions remained quite constant (Table 5). In Long Pond between May 28

through June 28 the ratio increased by .10 and in Wood Pond by .06 between June 17 and July 1. The ratios increased although both the standard length and body width decreased upon commencement of metamorphosis.

Standard Length - Body Depth

Growth of tadpoles in the vertical plane (body depth) appears to be isometric with that in the longitudinal axis. Standard length - body depth ratios were similar for the two ponds and did not vary to any extensive degree (Table 6).

The growth of the tadpole's body in girth and length appears to be isometric.

Hind Limb Growth

The growth of hind limbs of tadpoles taken from Long Pond and Wood Pond (Figure 3) followed a very similar pattern. The most striking difference was that seen between the total lengths of the limbs on animals from the two ponds. The hind limbs of Long Pond tadpoles (July 6) were on the average 6.4 mm longer than those collected in Wood Pond (July 5), (Table 3g).

The growth curves plotted in figure 8 illustrate the initial slow growth of the hind limbs with a sudden acceleration in the latter part of June producing hind legs that were equal to 95 percent of the standard length in Long Pond on July 6 and 75

percent of the standard length in Wood Pond on July 5. They had increased to 144 percent by July 12 in Long Pond and 127 percent in Wood Pond by July 9 (Table 7, Figure 4).

Ontogeny of the Hind Limb Bud

The account that follows is based on Long Pond tadpoles, however events in Wood Pond were very similar.

Limb buds were first noted on animals ranging from 10-17 mm in total length on animals taken from Long Pond on May 28. Between May 28 and June 28 the limbs increased very little, growing to 5.9 mm in June, (Appendix 1).

The femur and tibia-fibula became evident when the limbs attained a length of 1 to 1.5 mm. In legs shorter than this, there was no flexure of the limb denoting the two major leg divisions just mentioned. Distally, the legs had become paddle-shaped at about this same time (1.5 mm).

Three toe primordia, the third, fourth and fifth, were noted when the hind limbs were about 2 mm in length. Usually by the time limbs had reached 3 mm, all toe primordia were present.

On July 6 the mean length of the hind limb was 26.6 mm. In the July 12 sample the average limb length was 30.4 mm.

Wet Weight Growth

The wet weight growth curves in both populations were somewhat similar in shape, the difference being the greater weights attained by Long Pond larvae (Figure 5). Long Pond larvae were significantly heavier in the third and fourth weeks (Table 3h). The maximum in Wood Pond was reached five days prior to that in Long Pond (Figure 5).

The mean wet weight of six tadpoles collected from Long Pond on May 28 was 23.5 mg. On June 18 the average weight was 657.6 mg., an increase of 2798.3 percent in 21 days. An average wet weight on July 6 was 2,296.0 mg. representing a 349.1 percent increase in 18 days. A marked decrease was seen in the sample taken on July 12 in which the mean weight was 1,407.8 mg., 38.7 percent less than the maximum.

Wood Pond tadpoles on June 17 averaged 735.0 mg. The July 1 mean was 1702.6 mg. an increase of 231.6 percent in 14 days. A decrease was seen in the July 5 mean, 2.6 percent. A greater decrease, 46 percent, was seen in the collection made on July 9 with a mean of 895.5 mg.

Dry Weight (Organic matter) Growth

Dry weight growth curves for Long Pond and Wood Pond can be found in Figure 5 and Tables 1i and 2i, respectively.

Table 3i illustrates the fact that Long Pond animals, except for the first week, contained significantly greater amounts of dry weight during the study.

A mean of 38.8 mg. was calculated for June 17 in Wood Pond. The sample collected from Long Pond on June 18 had a mean of 24.2 mg.

Larvae collected from Long Pond on July 6 averaged 222.7 mg. an increase of 920.2 percent. Animals from Wood Pond on July 5 averaged 145.8 mg. an increase of 375.8 percent. Those animals taken from Long Pond on July 12 had a mean of 188.3 mg., a loss of 15.5 percent of the maximum dry weight. Wood Pond animals on July 9 had a mean of 102.4 mg., a decrease of 29.8 percent.

Ash Weight Growth

Ash weights of animals from Long Pond were significantly greater than those collected from Wood Pond during the entire four week study (Table 3j, Figure 5).

The mean for a sample of tadpoles taken on June 18 from Long Pond was 5.2 mg. Animals from Wood Pond on June 17 had a mean of 2.4 mg.

For a sample of tadpoles collected from Long Pond on July 6 the mean was 33.4, an increase of 642.3 percent over the June 18 sample. The mean of a

sample of larvae collected from Wood Pond on July 5 exhibited a mean of 18.5 mg., increasing 770.8 percent over the June 17 mean.

A subsequent decrease was observed in both ponds. On July 12 a sample from Long Pond had a mean of 23.1 mg., a decrease of 30.2 percent from the maximum. The mean of a collection from Wood Pond on July 9 was 12.2 mg., a loss of 34.2 percent from the maximum.

Water Content and Weight Loss

An inverse relationship between time and body water content existed for tadpoles from both ponds (Figure 6). For the first collection date the larvae in Long Pond contained a greater percentage of water (97.8 percent) than those taken from Wood Pond (95 percent). Larvae in later collections contained similar water percentages; in fact, percentages of water in the larvae from the two ponds after the initial collection were very nearly identical (Table 8). A steady decline in water content was observed through commencement of climax metamorphosis when on July 9 in Wood Pond larvae the water content was 88.6 percent and 88.0 percent in larvae from Long Pond on July 12.

From a maximum wet weight on July 6 there was a 38.6 percent loss on July 12 in Long Pond. This was accompanied by a 15.8 percent loss in dry weight.

Of the total weight lost, 96 percent was loss in water content and 4 percent was dry matter. The means of two young-of-the-year collected on August 3 was still 49.1 percent below the maximum weight observed.

A 47.4 percent wet weight loss on July 9 was measured in Wood Pond larvae. The dry weight loss was 29.7 percent and did not occur at the same time as the wet weight loss since the dry weight and ash weight reached a maximum four days after the wet weight maximum was observed (Figure 5). The wet weight loss was comprised of 95 percent water and 5 percent dry matter. On July 30 a sample of 4 young-of-the-year averaged 55.1 percent less than the maximum in Wood Pond.

In contrast pre-adults and adults from Wood Pond averaged 77.64 percent and those from Long Pond averaged 78.14 percent water.

Maximum Size Records

Tadpoles in Long Pond reached an average total length of 61.4 mm on July 6, the highest average in both ponds. The longest animal was 64.1 mm in length.

Larvae in Wood Pond on July 5 attained a high average of 56.1 mm. The greatest length attained by a tadpole was 63.9 mm.

Long Pond animals had the greatest average standard length of both ponds, 27.8 mm., on July 6. The greatest

standard length (35.0 mm) occurred in the tadpole also exhibiting the greatest total length.

The larvae in Wood Pond had their greatest mean standard length (22.7 mm) on July 1, four days before the record total length was observed on July 5. The record standard length was 24.8 mm.

The mean wet weight record was reached on July 6 in Long Pond at 2296.0 mg. A weight of 2602.6 mg. was attained by a tadpole on June 28, the heaviest animal observed.

Wood Pond larvae were heaviest on July 1 with a mean of 1702.6 mg. On July 5 the heaviest tadpole observed had a wet weight of 2170.0 mg.

Larvae having the greatest amount of dry matter (organic and ash) content were those from Long Pond. On July 6 a mean of 222.7 mg. was calculated and the individual with the greatest value, 259.1 mg. was observed in the same collection. Wood Pond tadpoles reached a high mean dry weight on July 5, 145.8 mg. The individual exhibiting the greatest dry weight (207.2 mg.) was in the collection of July 5.

Animals in Long Pond contained 33.4 mg. of mineral on July 6, the highest mean of the two ponds. The individual with the greatest amount of mineral, 37.3 mg., was observed on the same day.

Wood Pond larvae showed a high mean of 18.5 mg. on July 5 and the tadpole with the greatest mineral content

was one possessing 29.6 mg. in the same collection.

Tooth Rows

Tooth rows are used by herpetologists to distinguish anuran species, this is one of the larval characteristics that appears in every key utilized in identification.

Rana sylvatica larvae have been characterized by 3 upper rows and 4 lower rows of labial teeth, designated by the formula 3/4.

In the course of the study, tooth row formulae were noted for the tadpoles. It was soon discovered that tadpoles which could otherwise be identified by other characteristics such as tail fin height, pigment pattern and blunt snout, exhibited extremely varied tooth row formulae. Formulae varied from 2/3 through 4/4 during the course of the study (Table 9).

The earlier stages showed the greatest variation in rows. In the later collections the formulae with the lowest tooth row numbers became increasingly more infrequent.

The similarity in the Wood Pond data for the first three collection dates is especially striking. On June 17 the tooth counts of 11 larvae were distributed as follows: 2/3 - 9%, 3/3 - 36%, and 3/4 - 55%. A sample numbering 22 animals on June 21 had an almost identical distribution; 2/3 - 5%, 3/3 - 40%, and 3/4 - 55% formula. The distribution of tooth row

formulae was again very similar - 3/3 - 36%, 3/4 - 55%, and 4/4 - 9%, for a sample of 11 larvae collected on June 26.

Larval Behavior

Larvae, upon hatching from the egg mass, remain in the vicinity of the mass, very often attaching to the jelly envelopes by means of the oral sucker. Here they may stay for two to three days apparently consuming the envelopes since in the laboratory these disappear within this time and examination of guts reveal the intestine packed with what appears to be gelatinous pieces. No evidence of fouling of the water is detectable that might be expected if the envelopes were merely decomposing.

Under laboratory conditions at about 19° C active feeding does not begin until about the fourth or fifth day following hatching. Presumably, commencement of feeding activities follow a similar schedule under natural conditions. Observations were made on a group of egg masses in Long Pond in 1966. Larvae were hatching and attaching to the masses on May 21 and the larvae were still associated with the masses on May 28. They appeared to be actively feeding on the envelope. Several algae were associated with the envelopes. Tetraspora was predominant among the algae and the larvae could conceivably have been consuming these.

Movement within the pond during early morning hours seemed to be related to water temperature. Collecting in Long Pond was usually unproductive until about 1000 when the tadpoles began appearing in the shallow water at the pond's edge. On the morning of June 14 which was cloudy, at 0900 tadpoles were very scarce and those that were seen, were resting on the dead sedges at the pond bottom. As the pond warmed further, the larvae began moving in the deeper water. They apparently spent the cool night hours under the last year's sedges which formed a solid carpet on the pond bottom. At least the animals were seen to come from beneath these old sedges upon sufficient warming of the pond. On cloudy days the tadpoles' appearance was delayed.

When the larvae did appear they rested either at the water's surface or about one inch below it. When disturbed the tadpoles usually dived for the tangled sedges at the bottom of the pond. They seemed to be very sensitive to shadows, diving as soon as the edge of one was cast over them.

By June 14 the larvae had begun to surface and gulp air. A tadpole would swim to the surface and gulp air, immediately diving to a depth of six inches. They would then level off at this depth and often remain motionless. An interesting observation was made on July 1 at Wood Pond. At 1015 the water

temperature three inches below the surface was 23.5° C. The tadpoles were swimming out from under a mat of decaying sedges, leaves, and small chopped twigs. They were surfacing and gulping air. The temperature at about the same depth under the mat was 21° C. The animals were concentrated at the west end under the shade of a canopy of alder, ash, and aspen. That end of the pond remained shaded during a greater part of the day.

Upon emergence of the forelimbs the larvae were found resting upon vegetation that projected above the surface of the pond. When disturbed these animals didn't hesitate in diving into the pond and remaining in seclusion. They seemed to be extremely wary and disappeared at the slightest disturbance.

Discussion

Measurement of the length in anuran larvae presents somewhat of a problem. If one uses the usual total length dimension he has to contend with the probability of encountering damaged tail tips which will influence the measurement producing an underestimation of longitudinal growth. This particularly becomes a problem with woodfrog larvae since they are cannibalistic when confined in small quarters; e.g., a collection jug. The use of the snout-vent length is somewhat more reliable because of its obvious exemption from cannibalistic

attrition. Another measurement subject to damage through confinement was the tail height. Often after a few hours the lower tail fin edges were shredded on some of the tadpoles.

There were several measurements studied that did not exhibit any significant differences between the populations except for week III when those animals from Long Pond exhibited greater dimensions. Among these were total length, tail length, tail height, interorbital distance and internaral distance. Comparison of these dimensions indicates that the individuals comprising the tadpole populations of Long and Wood Ponds were similar. There are three possible explanations for the significant differences that were seen in Week III. One is the disparity in the time at which the samples were collected. The sample from Long Pond was taken two days after (June 28) that taken from Wood Pond (June 26). Perhaps the difference of two days was sufficiently great to cause the significant differences seen between the two ponds. Interestingly, the mean of the total length of a sample collected from Wood Pond on July 1 was still 2.7 mm shorter than the June 28 Long Pond sample mean. The tail height was 1.8 mm shorter in the July 1 sample than the Long Pond sample collected on June 28. The interorbital distance was 1.6 mm less in the July 1 sample than the Long Pond sample collected on June 28.

The internaral distance was .3 mm narrower in the July 1 sample than the June 28 sample. The .2 mm difference between the two ponds in Week III was highly significant. These comparisons, although the Wood Pond sample (July 1) had the time advantage over Long Pond (June 28), indicate that very probably the 48 hour time difference, was not as important as first suspected. The standard length in Wood Pond increased by only .3 mm between June 26 and July 1 and decreased .8 mm between July 1 and July 5, whereas in Long Pond it increased through July 6 and then decreased on July 12. Perhaps the population in Wood Pond had entered into a later stage of metamorphosis since the standard length had already begun to decrease. During the first part of the third week temperatures in both ponds were low (Figure 3). The high for June 25 in Wood Pond was 48° F and the low for the 26th was 38° and on the 27th reached a low of 37° F. The low temperature on the 27th in Long Pond was 61° F, although considerably cooler than the lows experienced previously, was still within normal survival temperature (Herreid and Kinney, 1967). Temperature regimes present in the ponds may have been responsible for differential growth rates in the ponds throughout the study. That in Long Pond was much more stable than the temperature record in Wood Pond and may have provided a more suitable environment for larval growth.

Temperature records in two Alaskan ponds in 1964 (Herreid and Kinney, 1967) were similar to those of the Itasca ponds under discussion. Ballaine S.R. was a smaller, shallower pond similar to Wood Pond and Ballaine II was a larger pond, deeper and similar to Long Pond. There is a striking similarity in total length growth curves and weight growth curves in the Alaskan ponds to those found in the ponds under discussion. Growth in total length and weight, which I presume is wet weight, in Ballaine II surpassed that in Ballaine S.R. just as happened in Long and Wood. This supports the hypothesis that the temperature regime may be a primary factor influencing the growth of larvae.

With the striking temperature differences seen in the two ponds it is surprising that climax metamorphosis appears to have occurred about the same time if not a bit earlier in Wood Pond (Figures 3 and 5, standard length and wet weight respectively). Due to the lower growth rate exhibited by the cooler Wood Pond population one might expect the animals to metamorphose at a later date. There may have been several factors involved in the bringing of the two ponds into metamorphic synchrony. The water level had been steadily diminishing in both ponds. From June 27 to July 8, a period of 12 days, .43 inch of rain fell, an amount that would not provide any appreciable quantity of runoff. This

amount fell during two showers, .07 on the 27th of June and .36 on July 3. Oosting (1956) states that light rains of 0.15 inch usually are intercepted by the vegetation and only heavy, fast rains will be involved in runoff. Wood Pond was dependent upon runoff as its major water source. This period of drought reduced Wood Pond to the small pool at the west end. The pond's drying up resulted in the formation of a pool that was thick with debris, probably causing crowding of the tadpoles. The decrease of water depth also submitted the pond to startling diel temperature fluctuations with high temperatures prevailing, one day the temperature of the pond reached 83° F. D'Angelo et al (1941) discovered that starvation following the middle prometamorphic period caused a speed-up of the metamorphic process. The animals in Wood Pond were past this developmental point since they had begun to show metamorphic changes such as increased hind leg growth (Figure 3).

With the limited light caused by the turbidity of the water and since the pond was drying the productivity of the pond may have been severely reduced thus limiting the amount of food available to the tadpoles.

Etkin (1964) stated that increased temperatures accelerated metamorphosis to a greater extent than growth within the range of 15 to 30° C. Conditions

in the pond were such that starvation was a definite possibility, the temperatures were high, and more than likely overcrowding occurred. All of these factors may have contributed to the early emergence of frogs of a smaller size than those in Long Pond.

Hind limb growth can provide a valuable landmark for estimation of the onset of climax metamorphosis (Etkin 1932). Hind leg growth in both ponds progressed at a rather slow rate until the third week when the Long Pond growth curve exhibited a very steep slope to the 6th of July and then began to level off between July 6 and 12, thereby approximating a sigmoid curve as was observed for Rana palustris by Etkin (1932). The growth curve in Wood Pond did not show as sharp an increase as was observed in Long Pond and was not sigmoid although the animals were metamorphosing. The rapid growth phase began at about 5 mm length which was the same length Etkin (1932) observed to mark the beginning of this phase. The fact that there was no sharp increase in hind limb growth with a subsequent rate decrease similar to that seen in Long Pond and observed by Etkin in lab-reared animals further suggests that the Wood Pond population may have been victims of the early summer drought. Perhaps ample rainfall might have allowed the Wood Pond tadpoles to develop for a longer time and produced animals with growth rates similar to those observed for tadpoles from Long

Pond.

The greatest dissimilarity between the tadpole populations from Long and Wood Ponds was evident in weight. Wet weights, although not significantly different for the first two weeks, were highly significantly different during Weeks III and IV. The animals in Long Pond were heavier than those in Wood Pond. Larvae from Wood Pond were heavier during the first week, however not significantly so.

There is no question that woodfrog tadpoles in Long Pond were significantly heavier in amounts of dry matter and mineral content. Only in the first week of the study were Wood Pond tadpoles significantly heavier. It is quite interesting that the ash/wet weight ratios (Table 10) are very similar to the values obtained by Etkin (1932) for R. palustris. This is in spite of the fact that Etkin removed the intestinal contents of his animals while the present data represent tadpole minerals and intestinal content minerals. The increasing ash weight/wet weight ratio is due to a combination of an increasing amount of mineral content probably attributable to the growth of the limbs of the animal and gradual ossification of the skeletal elements and to the gradual loss of body water. That the ratios are similar is not surprising since the body structures of R. palustris and R. sylvatica are very similar, at least in gross

appearance.

Although dry weights were very different between the two ponds, dry weights expressed as percent wet weight, were similar for both ponds (Figure 6). The only great dissimilarity was during the first week. If the dry weights had been unduly affected by intestinal contents one would expect to see an effect in larval growth curves and the larvae from the two ponds would not have exhibited such similar dry weight percentage growth curves. It seems highly unlikely that tadpoles from both ponds would contain similar amounts of intestinal material on each collection date. If the intestinal contents were influential, very different weight percentage curves should have been obtained. Unfortunately, Etkin does not state the weight of the material that was removed from the intestines of the tadpoles.

Perhaps, the weight differences seen between the two populations, particularly the dry and ash weights, may be attributed to the vegetation in which the ponds were located. Long Pond was situated just slightly northeast of the Biological Station Campus with aspen being the common tree on the west edge of the pond and a mixture of red pine and aspen on the east edge. In contrast Wood Pond lay in a spruce-fir stand. Consequently, runoff in Wood Pond may have been considerably poorer in nutrients because of the large

coniferous area drained by the pond. Coniferous needles are known to be poor in magnesium, calcium, and potassium ions (Daubenmire, 1959). On July 5 the pH in Wood Pond was approximately 5.7, and 6.7 in Long Pond on July 6. Both measurements were made at 1400. Total alkalinity in Long Pond on July 6 was 128 ppm and in Wood Pond on July 5 was 32 ppm. Carbonates are primarily responsible for the alkalinity of the ponds.

The water content of tadpoles in both ponds was high at the beginning of the study and then there was a gradual loss of water throughout the rest of the study. In contrast the amount of dry weight increases gradually. The dry and ash weight curves for Wood Pond continued increasing on July 5 but the wet weight had decreased. Perhaps the hind limb and forelimb growth was influential in this phenomenon since hind limb growth was still rapid and had not leveled off. Over 800 mg. of weight were lost by tadpoles in both ponds between the last collections and those just prior to the last collection. Since only 5 percent of this loss was due to dry weight, this indicates that the greatest part of the weight loss observed during metamorphosis is due to water loss. Adolph (1931) also observed this phenomenon in laboratory animals.

Maximum sizes, weights, etc. are frequently the

only data that one has to compare with other people's values, and some comparisons are possible in this instance for Alaskan and East Coast animals. The high average of 61.4 mm surpasses the maximum mean length of 60 mm observed in Alaskan woodfrog tadpoles in 1964 (Herreid and Kinney, 1967). The longest tadpole observed from Long Pond in 1966 was 64.1 mm long. A Wood Pond tadpole 63.9 mm was also longer than any reported from Alaska. Alaskan animals, on the other hand, averaged heavier than northern Minnesota tadpoles. The heaviest Alaskan average was 2.85 g. as opposed to the high average of 2.30 g. from Long Pond. The heaviest tadpole observed was 2.60 g., considerably lower than the mean of tadpoles from Alaska. In fact, in two out of three Alaskan ponds the average maximum weight exceeded that of the Itasca Park animals. Northern Minnesota tadpoles are longer and weigh less than those in Alaska. Adolph (1931) observed a maximum weight of 1.23 g. for laboratory-reared tadpoles; presumably these were New York animals since he did the work at Rochester, New York. If this is true, eastern woodfrog tadpoles may be considerably smaller than those from the western portion of the species range. Wright and Wright (1949) state that the length of New York tadpoles is 49.8 mm. Hinckley (1882) observed a maximum total length of 58 mm for Massachusetts animals. One must exercise caution when comparing laboratory reared animals with

wild animals since crowding effects, which are well known for laboratory-reared anurans but have never been conclusively demonstrated in the field, may affect the maximum size attained. Adolph (1931), on the other hand, shows a growth curve for an animal grown alone whose maximum weight was 1.23 g. Perhaps this specimen also represents Adolph's maximum weight recorded for his laboratory reared animals since his stated maximum was 1.23 g. It seems unusual for the smallest tadpoles to eventually produce the largest adults in the eastern part of the range and vice versa in the western portion of the range.

Perhaps the following may be an explanation. Breeding may occur from March 19 to April 30 at Ithaca, New York and as early as February 20 in West Virginia (Wright and Wright, 1949). In "normal" years breeding occurs in northern Minnesota and Alaska at approximately the same time, late April to early May (Kessel 1965; present study 1968). The advent of spring as measured by the arrival of the thaw occurs on April 15 in upstate New York and about May 1 in northern Minnesota (Kimble 1961). Since woodfrog breeding is apparently related to thaw (Kessel 1965), this would mean at least a two week earlier breeding date for New York animals.

The two week to four week head-start would allow an early metamorphosis, possibly as early as June 8

(Wright and Wright, 1949). The young-of-the-year would then be entering their terrestrial phase at a time when food organisms may be more abundant than at the time when northern Minnesota animals emerge (early July). The extra growing time might provide the necessary boost needed to produce larger adults in the east. Indeed, the longer growing period for young-of-the-year, as a result of early breeding may benefit adult growth.

Perhaps an increase in tadpole size has been a compensatory adaptation of the poikilothermic woodfrog for the decrease in growing season afforded the young-of-the-year in northern regions. The fact that the larval stage is aquatic thereby may allow an increase in size that would otherwise be untenable if the larvae were terrestrial. Surface/volume relationships would not be as important since the water would act as an insulator against drastic changes.

It may be that a large tadpole produces a relatively large young-of-the-year, which may be necessary to produce a minimum overwintering size due to the short growing season.

A nearly constant relationship of the standard length/total length was discovered when these ratios were calculated for the two populations. The means were very similar, .445. These values remained the same throughout the pre-climactic metamorphosis

period.

The ratio between the standard length/body width was discovered to be very nearly constant in the two populations. The mean value for Long Pond was 1.67 and 1.69 for Wood Pond.

A nearly constant relationship was observed between the standard length and body depth. The means were nearly identical, 2.31 for Long and 2.32 for Wood Pond. The increase on July 6 in Long Pond was due to the eruption of forelegs in some of the larvae. It appears then that in these dimensions, growth in the longitudinal axis (standard length) is isometric or very nearly so in regard to the girth dimensions (body width and body depth). The latter ratios, since they are fairly constant, may be useful as aids in identifying preclimax woodfrog tadpoles.

As has been noted by other workers, some anuran species exhibit variable numbers of labial tooth rows (Bresler and Bragg, 1954; Bragg and Hayes, 1963). Certain species may also add tooth rows with increases in length (Bresler and Bragg, 1954). Rana sylvatica tadpoles exhibit an extremely wide range of tooth row formulae including the so called "typical" formula 3/4 (3 upper and 4 lower rows). The early collections contained animals with tooth formulae ranging from the "typical" R. pipiens formulae, 2/3, 3/3, to the "typical" R. sylvatica formula.

The greatest number of formulae seen in a single collection was four. As the tadpoles matured the individuals in the samples more frequently possessed the "typical" formula and even surpassed it with a 4/4 formula and an inverse, 4/3 formula.

The extreme similarity in sample composition observed in the first three samples collected from Wood Pond is very intriguing. Long Pond samples, in contrast, were characterized by a wide array of tooth formulae.

If one assumes that tooth formulae change with age and/or length of tadpoles, the differences seen between the ponds might be explained. From research, presently underway, it appears that tooth rows do increase with age and total length.

The series of rather homogeneous tooth formulae observed in samples from Wood Pond suggest that perhaps these tadpoles originated from groups of egg masses that were deposited within a short period of time, during a single breeding session. Since the pond is well protected and probably not exposed to the early thaw that more open breeding ponds such as Long Pond experience, it may be one of the later ones to become available for breeding. This would probably limit breeding in this pond to a single session. Tadpoles of such a single deposition would possess more homogeneous tooth formulae since they

would be more nearly alike in age.

Heterogeneous tooth formulae observed in Long Pond samples can be explained if multiple breeding sessions occurred. More than one session did occur since breeding activities in 1966 were interrupted in late April by a week of cool weather and were again initiated in early May following this unfavorable period. Proof of more than one session was the observation of egg masses in the same pond that were in markedly different stages of development. More than one breeding session was observed for Long Pond in 1967 and 1968, as well. Samples drawn from the Long Pond populations would reflect the tooth formulae associated with variable ages. They would be more variable because of the wide range of ages.

TADPOLE DESCRIPTION

Rana sylvatica tadpoles are small compared to other ranid species which, according to Wright and Wright (1949), range up to 149 mm. In Itasca State Park in northern Minnesota in 1966 the maximum length was 64 mm with a mean length of 61 mm. The standard length or snout tip to the posterior edge of the anal canal piece was 45 percent of the total length or 27.5 mm in the case of the mean maximum length. The standard length - total length percentage relationship is maintained throughout the larval phase.

One of the most distinctive features of the woodfrog tadpole's anatomy is the high tail crest (see Figure 7). The greatest crest height was 16 mm. Usually the height of the dorsal portion of the tail crest exceeds that of the ventral half. Crests often grow so that the margins increase in length faster than the part attached to the musculature and therefore appear to be ruffled. Contrary to Wright and Wright's (1949) statement that the dorsal crest extends to the "vertical of the spiracle", the crest on the tadpoles examined during the present study extended approximately 3/4 of the distance between the "vertical" and posterior edge of the anal canal piece. It is true

that the greatest crest height is in the cephalic half of the tail (Wright and Wright 1949).

The slope of the tail musculature is continuous with the dorsal slope of the body which presents a graceful sloping curve in the hind-portion of the tadpole. Commonly, the long axis of the tail musculature exhibits a slight upward tilt (see Figure 7). The musculature begins to taper from its insertion on the body as stated by Wright and Wright (1949).

The upper 1/4 to 1/3 of the musculature is heavily pigmented with clustered melanophores as shown in the figure. In contrast, the lower portion appears considerably lighter due to the dispersed nature and reduced numbers of melanophores. Heavier mottling on the dorsal crest is caused by a greater number of melanophores than are found on the ventral portion of the crest. On the ventral half of the crest the melanophores are sparse and tend to be drawn into thin lines in contrast to those dorsally which are stellate and clumped. These lines tend to follow branches of the circulatory system and are quite common in both dorsal and ventral crests in older tadpoles. A portion of the ventral tail crest in the vicinity of the anal canal piece (see Figure 7) is devoid of pigment cells. The absence of pigment cells prevails on the ventral surface of the body of the tadpole, thereby producing the characteristic translucent belly of the

woodfrog tadpole. Along the edge of the dorsal crest is an almost continuous border of very closely spaced melanophores giving the appearance of a black margin. At the tail tip are very closely spaced melanophores giving it a dusky appearance.

Another feature of the tail is the occurrence of two to six pulsating "lymph hearts" on either side and attached to the caudal veins. The position of the lymph vessels as well as the vein is marked by a concentration of melanophores.

It is possible to see the internal organs through the ventral surface since the skin layers are not invaded by the other two pigment cells found in frogs, guanophores and xanthophores. This is in contrast to other species whose internal organs become obscured early in development with the latter pigment cells. During the period of prometamorphosis the peritoneum is invaded by a solid layer of xanthophores, which is then externally covered by a layer of guanophores, eventually obscuring the view of the abdominal viscera ventrally.

The tadpole has a generally brownish hue; i.e., the ground color is brownish. Very probably, the brownish cast is caused by the extremely numerous, minute spindle-shaped melanophores that are almost universally scattered over the entire body. Two pigment cell types are most prevalent on the dorsal

surface of the body - melanophores and xanthophores. The overall impression is that the body, when the pigment cells are expanded, is mottled black with gold spots (xanthophores). The mixture extends toward the snout, however melanophores become the more numerous cell type. Because the cells are fewer, the snout has a lighter appearance. Guanophores are the scarcest cell type dorsally but in later development account for the white belly seen in the woodfrog and in many other anurans.

The area of the spiracle is less darkly pigmented than the rest of the body and the tip of its orifice is unpigmented.

Delimiting the pupil of the eye is a ring of xanthophores; the eyeball is liberally sprinkled with xanthophores.

The oral fringe consists of a double row of lobes attached to a single oral "bib" below the lower beak. An indentation occurs at the bottom of the "bib" (see figure 7). In young tadpoles the fringe is sparsely sprinkled with melanophores. As the animals age, the lobes are more heavily pigmented. Above and lateral to the upper rows of labial teeth on either side are fan-like groups of six or seven lobes. These lobes are the most heavily pigmented of those around the mouth.

All upper and lower labial tooth rows except the

first upper row are attached to fleshy elongate bars. Attachment of the first row is on the overhanging "lip" of the tadpole. The second row is very commonly inserted under the first row and the third row under the second so that usually, the upper number cannot be determined unless the outermost rows are lifted out of the way. Therefore, the upper rows in the figure are diagramatic. Lower labial tooth rows, on the other hand, are depicted as they appeared. As has been mentioned in a previous section the tooth row numbers showed considerable variation. Upper row numbers ranged from 2 to 4 and the lower rows were 3 or 4. All combinations of the variations were observed although the typical had been reported as 3/4 (Wright and Wright 1949, Orton 1952).

The configuration of the upper tooth row is very similar in all tadpoles and often variability is apparent only in the number of teeth on the fleshy bar.

Lower rows exhibit considerable variation in their disposition. A break appears in the first row when the tadpole is examined grossly; it is due to the row's being placed on two adjacent lobes (see figure 7). A variation which is very common in young tadpoles (almost 100 percent in laboratory reared animals) until a length of about 13 mm is reached, is an undissected first row. As the tadpoles grow, apparently the row is divided by the diverging lobes

and the unsplit row becomes a rarity in older, 28 mm or greater, tadpoles (8 percent in laboratory reared animals). Other variations, less numerous, such as double, triple and quadruple dissections in the first row were observed. The second and third rows were normally entire and were much less commonly split. A break in the third row was more common than in the second. Variability in the fourth row was manifested primarily in the length of the fleshy bar. The length of the bar was sometimes only wide enough to hold two teeth, however sometimes the fourth row was as long as 3/4 the length of the third row. Most commonly, the relative length observed was similar to that shown in the figure.

STRIPE POLYMORPHISM

Introduction

Several amphibian species exhibit a polymorphism for a striped dorsal pattern and those that have been investigated have been discovered to be due to a dominant gene. The dominant allele produces the striped phenotype and the recessive gene results in a different pattern or in a patternless animal (Goin 1947, Lantz 1947, Moriwaki 1953, Moriya 1952, and Pyburn 1961).

Some Rana sylvatica populations possess a pair of alleles with a similar genetic and phenotypic relationship, the striped phenotype controlled by a dominant gene and the nonstriped by its recessive allele (Browder et al. 1966).

Striped individuals, both larvae and adults, possess an unbroken mid-dorsal cream colored stripe which extends from the snout to the end of the urostyle. Usually similar stripes are present on the femurs and tibia-fibulae of these animals. Individuals lacking the dorsal stripe do not have femoral or tibia-fibular stripes.

The stripe frequency in the woodfrog displays considerable regional variation. The frequency ranges

from 100 percent non-striped individuals in the eastern part of its range, from Labrador south along the East Coast to western Virginia, North Carolina and Georgia; westward to Illinois, Wisconsin and dipping into Missouri and the northwest corner of Arkansas. Striped frogs occur throughout the remainder of the woodfrog's range, as far west as Alaska, north to the Arctic Circle, south almost reaching the United States border in Manitoba, throughout the Canadian Provinces with exception of the Northwest Territory where it is absent from the northeast half. In the United States the striped phenotype occurs from Wisconsin through Minnesota, with the exception of the southwestern counties, into North Dakota's northwestern quarter and into Canada. The frog's range then extends into most of Montana with exception of a narrow section in the eastern portion, into the mid-portion of Wyoming and dips into the north central mountain area of Colorado (Martof and Humphries 1959). Stripe frequencies range from below 50 percent in the eastern portion of its range to well above 50 percent in the northwestern part of its range.

The present study was designed to investigate the frequency and distribution of the stripe gene in a restricted area of Minnesota, the Itasca Park region. The occurrence of quite diverse habitats within the Itasca region indicated that it might be a most

favorable area in which to carry out the present study. In addition, the frequency in the area could be compared with frequencies from other areas in the state.

During the past 40 years samples have been collected from various areas in Itasca Park and from other parts of the state. Many of these collections do not lend themselves to detailed analysis. The present study was designed to test the effect of season, habitat type, age class structure, and possible differential mortality and survival on the frequencies of the two phenotypes, and at the same time it was hoped that some knowledge of the adaptive value of the two phenotypes might be gained.

Materials and Methods

The study of the stripe polymorphism in Rana sylvatica was initially undertaken during the second summer session at the Itasca Biological Station in 1966. Systematic collections were made from Long, Wood, and Twin Ponds (Figures 1, 8 and 9). Because of their limited accessibility, Bog D Trail Pond and Mary Creek were sampled once during the period of July 17 to September 17, 1966. The 1966 collections were made to determine the extent of the variation in the stripe frequency in the Itasca Park area.

On June 14, 1967, an investigation of possible

seasonal shifts in stripe frequencies was initiated. Extensive collections were made from La Salle Pond, Campground Pond, and Campground Chain Ponds (Figures 9 and 10). These ponds were considered to be representative of Mixed boreal habitats. As many frogs as possible were collected during each sampling period. Animals scored in the field were sexed, measured for standard length (snout-urostyle), tibia-fibula length, scored for the striped and non-striped phenotype, toe-clipped for future recognition and released. Recaptures were noted and all specimens were remeasured before they were released. Subsequent sampling was carried on throughout the latter part of July and August and the animals were released.

Similar collections from Bog D Trail Pond were made in June, July and August and from Mary Creek in June and August (Figures 11 and 12). Both are coniferous habitats.

Specimens from the James Ford Bell Museum of Natural History were examined for phenotype, measured and locality data were recorded. The distribution of these frogs is presented in Figure 13 and in the county list (Table 11).

Data were treated statistically by means of contingency tables. The term "resident frog" as used in the results section refers to a woodfrog that was a member of the population prior to the time of

completion of metamorphosis by the young-of-the-year.

Results

The striped phenotype occurs in 20 of 31 counties from which Rana sylvatica has been collected. The stripe gene is present in the northwestern and north central counties of the state (Figure 13). Of the five counties in the northeastern portion of the state, only in the most eastern, Cook County, is the stripe gene absent. All of the counties north of the Mississippi River on the eastern border contain woodfrogs and three of these are populated by the striped morph (Figure 13). Nonstriped frogs have been collected from three counties south of the Mississippi; Hennepin, Scott, and Rice counties (Figure 13).

The statewide stripe frequency was 17.6 percent, however this value includes Itasca Park animals which comprise 89 percent of the total number of animals available from the state. As one might expect, the frequency of 16.7 percent found for the Itasca region may have resulted in a biased state estimate.

Six county (Becker, Beltrami, Chisago, Clearwater, Hubbard, and Marshall) frequencies were compared for stripe frequency differences. The frequencies ranged from 15.2 percent to 32.1 percent. The differences among the six were highly significant ($p<.005$, Table 12).

A more detailed analysis of the samples from the

areas in the habitats, coniferous and mixed, already described for the Itasca Park region, was carried out. No significant seasonal shifts in the stripe frequencies occurred around the five ponds sampled in 1967. When the data from all areas were pooled for each of the three months and compared, the differences found were not significant ($.25<p<.50$, Table 13).

Comparisons of annual samples from various localities in Itasca Park were made. Data were available for a comparison of two years' frequencies for the Mary Creek area - 1965 and 1967. The stripe frequency in 1965 was 18 percent and 17.4 percent in 1967. The difference between these two years was not significant ($.90<p<.95$, Table 14a).

A series of samples for four years was available from the Bog D Trail Pond area - 1964-1967. Stripe frequencies increased from 15.8 percent in 1964 to 21.9 percent in 1967. The differences between the frequencies for the four years were not significant ($.25<p<.50$, Table 14b). The two years exhibiting the greatest difference, 1964 and 1967, when compared, had frequencies that were not significantly different ($.950<p<.975$, Table 14c).

An analysis of the four year accumulation of frequencies for La Salle Trail Pond resulted in a Chi-square value, the probability of which was

.25 p .50, not significant. Stripe frequencies ranged from 15.2% in 1961 to 26.7% in 1965, (Table 14d).

Icehouse Pond, a small woodland pond situated on the campus of the Itasca Biological Station (Figure 8) has been sampled for a number of years. An analysis of four years' frequencies revealed no significant differences among them ($.975<p<.990$, Table 14e).

Since collections were taken from ponds located in two different habitats, mixed coniferous-deciduous and coniferous woods, pooled data from ponds in each habitat were compared. The hypothesis being tested was that one of the phenotypes might be better adapted to one of the two habitat types. Three of the ponds, Campground Pond, Campground Chain Ponds, and La Salle Pond, were pooled as a mixed coniferous-deciduous forest community (see Figures 9 and 10) and the other two areas, Bog D Trail Pond and Mary Creek, as coniferous communities (see Figures 11 and 12). Stripe frequencies in these two communities were not significantly different ($.50<p<.75$, Table 15).

During the field collection it was noticed that juvenile and adult stripe frequencies from the same area often differed considerably. It was also noted that adult-juvenile ratios appeared to differ between the two habitats. To establish a criterion for separating juveniles from adults, standard lengths of frogs for June, July, and August of 1967

were plotted against numbers of frogs. The histogram based on frogs taken in August was the most clear-cut; two discrete groups were evident (Figure 14). One consisted of animals ranging from 22 to 31 mm, which were obviously young-of-the-year. A complete break occurred between 31 and 34 mm. The second group ranged from 34 to 52 mm. The most logical interpretation of the two groups is that these represented yearlings and older frogs. A single group occurs in the June and July histograms, which seem to show a natural break at 37 mm. The dividing point agrees rather well with the findings of Bellis (1959) who placed the point at 36 mm. Using 37 mm as the cutoff point the animals were categorized for the two habitat types. Comparisons of frogs from mixed and coniferous communities which were subdivided into striped, nonstriped categories, were made for the months of June through August. During no month were significant differences found between adult and juvenile stripe frequencies. The p values ranged from .10 to .995 (Table 16).

In the mixed woods the frog populations sampled consisted of 41.0% juveniles whereas in the coniferous communities the percentage was considerably higher 71.4%. The difference was highly significant (p .005, Table 17).

As a further refinement, the hypothesis that age

differences occurred throughout the summer between the two habitat types was tested. In June, frog populations consisted of 30.4% juvenile animals in mixed woods communities compared to 68.9% in coniferous habitats. The difference was highly significant ($p < .005$, Table 18).

July populations in mixed woods consisted of 49.1% juveniles and 78.8% juveniles in coniferous communities. The difference between these was again highly significant ($p<.005$, Table 18).

Juveniles comprised 81.2% of the August population in mixed woods and 65.2% in coniferous woods and the frequencies did not differ significantly ($.10<p<.25$, Table 18).

Gene frequencies can be determined from phenotypic ratios through the use of the Hardy-Weinberg formula, $p^2 + 2pq + q^2 = 1$, where $p^2 + 2pq$ represents the striped phenotype and q^2 represents the nonstriped phenotype. P is the dominant gene frequency which is the striped gene, hence the heterozygotes (pq) represent a portion of the striped frogs. Q is the recessive gene frequency. The relationship of the gene frequencies is as follows: $p + q = 1$.

There are several underlying assumptions associated with the Hardy-Weinberg Law. These are: 1. random mating where on phenotype is not preferred as a mate over the other phenotype; 2. the genotypes

are at equal selective advantages; 3. migration of the alleles is equal; 4. mutation rates of the alleles are either nonexistent or such that they are in equilibrium. In short, if a population is in equilibrium, the Hardy-Weinberg Law is valid. Seldom are all, and more frequently none, of these prerequisites except random mating met. Although this is true, the law is still useful in gaining an insight into genetic constitution of a population.

Knowledge of gene frequencies, especially for a series of years from the same areas may give an indication of stability, in turn reflecting changes in selection pressures.

Icehouse Pond, with one of the lowest stripe frequencies, exhibited a stable frequency at about $p = .05$ and $q = .95$ and has been approximately the same for the eight year period covered by the samples studied (Table 19).

The Mary Creek population exhibited identical frequencies, $p = .09$, $q = .91$, for the two years, 1965 and 1967 (Table 19).

La Salle Trail Pond, with the exception of two years, 1964 and 1965, had frequencies identical to those of Mary Creek; $p = .09$, $q = .91$ (Table 19). In these two years $p = .14$, $q = .86$, however, sample sizes were relatively small, 15 and 23.

Bog D Trail Pond animals have exhibited

increasing stripe gene frequencies during a four year period as follows: .08 - 1964; .09 - 1965; .10 - 1966; .11 - 1967 (Table 19).

Gene frequencies were calculated for populations from the Itasca Park area and compared with three counties bordering Itasca Park and with Chisago County, which forms part of the mideastern Minnesota-Wisconsin border. These collections span eight years (Table 12) and were used because they represent the only samples adequate for statistical analysis. Itasca frequencies showed a dominant gene frequency of .09 with a recessive frequency of .91 (Table 19). Even though Itasca State Park extends into Becker County, a sample taken from the Detroit Lakes area (Figure 13), 60 miles southwest of the park in Becker County, revealed frequencies p = .14, q = .86, different from those in the park (Table 19). Two counties, Marshall and Beltrami, are situated north of the Itasca Park region. The southern portion of Beltrami borders both Hubbard and Clearwater Counties in which Itasca Park is located. Samples taken from the Mud Lake Refuge and Whiskey Jack Lake in the eastern portion of Marshall County and the Moose River in Beltrami County exhibited gene frequencies, p = .18, q = .82, higher than the frequencies exhibited by samples from the Itasca Region and southwest Becker County (Table 19). The gene frequency estimated from

a sample from Chisago County was similar to those of the Itasca Region, although the area is approximately 155 miles southeast, p = .08, q = .92 (Table 19).

The question arises as to what mechanism is involved in the maintenance of the polymorphism. The distribution of the genes can be determined by inserting gene frequencies into the Hardy-Weinberg formula, $p^2 + 2pq + q^2 = 1$.

If S, the stripe gene, is advantageous it might be slightly more so in the heterozygous condition due to heterosis. This would then place both homozygotes at a disadvantage which could maintain a balanced polymorphism.

Selection need not involve the phenotypes directly. The striped phenotype is not necessarily advantageous in itself but the gene may confer some physiological advantage or advantages on its possessor. In this way the problem of selective advantage would remain cryptic.

To illustrate the distribution of genes in two populations very different from each other in gene frequency, geographical location, and habitat, we can look at populations of frogs from Marshall and Chisago Counties. The latter samples have the highest and lowest stripe gene frequencies and are the most widely separated groups in Minnesota. For a population of 1000 frogs with a gene frequency

equal to that of Marshall County, 32 would be homozygous dominant, 295 heterozygotes, and 672 homozygous recessive woodfrogs. A similar sample of 1000 frogs from Chisago County would theoretically be composed of 6 homozygous dominants, 147 heterzygotes, and 846 homozygous recessives. Homozygous dominant genotypes are five times more numerous in Marshall County than those in Chisago County and heterozygotes two times more numerous in Marshall County than Chisago.

In the Bog D Trail Pond population one might expect to find the genotypes in the following ratios: 12 homozygous dominants, 196 heterozygotes, and 792 homozygous recessives.

Stripe gene frequencies in tadpoles, newly metamorphosed frogs, and resident frogs can be compared in a few instances. Larvae taken from Wood Pond on July 5 and 9, 1966, consisted of 7 (39 percent) striped and 11 (61 percent) nonstriped animals. Resident frog frequencies for July 30 to August 30, 1966 were 25 percent (5) striped and 75 percent (15) nonstriped. The differences were not significant (Table 20b).

Of Long Pond larvae taken on July 6 and July 12, 1966, 4 (18.1 percent) were striped and 18 (81.9 percent) were nonstriped. The frequencies for resident frogs for the period July 30 to September 17 were 16.8 percent (21) striped, 83.2 percent (104) nonstriped. The differences were not significant

(Table 20a).

The stripe frequency of newly metamorphosed frogs from the Campground Chain Ponds on July 23, 1967, was 16.8 percent (15) striped animals and 83.2 percent (74) nonstriped animals. Resident frog frequencies for June 23 to July 23, 1967 were 20 percent (45) striped and 80 percent (180) nonstriped. The differences were not significant (Table 21a).

In a sample of 116 newly metamorphosed frogs taken from Wegmann's Pond on July 29, 1967, there were 15 (12.9 percent) striped animals and 101 (87.1 percent) nonstriped animals. On June 16, 1967, in a sample of resident frogs 14 (16.4 percent) were striped and 71 (83.6 percent) were nonstriped. The differences were not significant (Table 21b).

In a sample of 82 newly metamorphosed frogs taken from Icehouse Pond on July 18, 1964, there were 4 (4.8 percent) striped and 78 (95.2 percent) nonstriped individuals. On July 24, 1964, 11 (15.9 percent) striped and 58 (84.1 percent) nonstriped young-of-the-year were present in a sample from the same pond. Six days later, on July 30, 1964, 4 (8.3 percent) of 48 young-of-the-year collected were striped, or an average of 9.4 percent striped in the July sample. Unfortunately, no resident frog samples are available for 1964, however the phenotypic ratios of the young frogs agree closely with percentages from

other years (Table 14e).

An unfortunate accident occurred on June 30, 1967, which afforded a comparison of the phenotypes as far as oxygen stress is concerned. Two samples of frogs, one taken from La Salle Pond and the other from the Campground Chain Ponds, were left overnight in the laboratory after scoring and marking. On previous occasions samples had been kept in plastic, insulated containers laid on their sides. These containers had screw cap covers provided with smaller flip top covers on pouring spouts. It was discovered that when the flip top covers were left open the frogs could escape even when the containers stood upright. For this reason the cap was left shut as before, however, apparently a number of frogs combined with a higher room temperature produced a high mortality. These frogs were preserved and later counted and scored. A X^2 test was used to compare dead frog stripe ratios. In neither case did the dead frog frequency differ significantly from the sample frequency (Table 22).

Discussion

Martof and Humphries (1959) prepared a map of the distribution of the woodfrog throughout its range. In Minnesota the pattern of distribution formed a double band of nonstriped animals separated by a central area inhabited by striped individuals. All

three bands were oriented in a northwest-southeast direction. When their map is compared with Figure 13, which was based on records (specimens used by Martof and Humphries) available from the James Ford Bell Museum in addition to personal records, the distribution of the striped phenotype presented by Martof and Humphries is incorrect. Striped frogs are extant for counties occurring in the "stripeless" areas of Martof and Humphries. Only Cook County in the northeast is stripeless and the sample sizes from Hennepin, Scott and Rice Counties hardly warrant inclusion as a "stripelss" area (Figure 13). Except for the eight specimens from these southern counties (south of the Mississippi River), there are no specimens in the museum collection from the rest of the southern "stripeless" area designated by Martof and Humphries. The specimen list (Table 11), gives one an idea of the type of woodfrog collecting that has been done in the past. Four counties in which the frog occurs are represented by fairly good samples (over 50), and three, Becker, Clearwater and Hubbard by an impressive sample size (Table 11). County totals represent sums of individual samples taken from that county. A county with a total of three animals could be made up of three samples of a single animal each, taken at widely spaced times from widely separated habitats within a county. Since counties vary

considerably in habitat diversity and size and since habitats may change or be changed in time, this sort of sampling is not adequate for strip frequency determination.

The strip gene in Minnesota appears to have a distribution that may eventually prove to be present throughout the state wherever Rana sylvatica occurs. Of the 11 county samples that do not possess the striped phenotype, all are represented by 10 or fewer individuals. In addition, these frogs were taken at widely separated times and localities.

It is interesting to examine the probability of collecting no striped frogs in the samples taken from those counties where the striped phenotype is absent. A table of binomial probability distribution compiled by the United States Bureau of Standards was used to find the following probabilities. It was assumed *that the stripe frequency was equal to that of the* state, 18 percent.

Two samples comprised the total of three animals from Anoka County. The probability of no striped frogs occurring in samples of one and two was .82 and .67, respectively. These three frogs were taken from the same area but two years apart. See Table 23.

The Carlton County total of ten animals was collected at seven different times spanning 23 years (Table 23). Five samples of single animals and a

sample of two and one containing three frogs were available. That a striped frog will not be present in a sample size of three may occur with a probability of .55. As stated before the probabilities of no striped frogs occurring in samples of one and two were .82 and .67 respectively. Four different areas within the county are represented.

Hennepin County is represented by two samples of a single frog each and Mille Lacs and Morrison Counties are represented by single frogs (Table 23). The probability of getting nonstriped frogs in samples of one has already been listed as .82.

A sample of two and three with a seven year span between collections constitutes the five animals from Cook County (Table 23).

Isanti's four animals result from a sample containing a single frog and a sample with three animals in it (Table 23).

Two samples, one with a single animal and the other with four frogs are extant from Lake of the Woods County (Table 23). The probability of no striped frog occurring in a sample of four is .45.

Pennington with a sample of two, Rice with a sample of a single animal and a sample of two animals, and Scott with a sample of three constitute the remainder of counties harboring nonstriped woodfrogs (Table 23).

In a sample of five animals a character could conceivably occur in 70 percent of the population with the occurrence of no animal exhibiting the character in the sample. Not until a sample size of 30 is reached does the lower sampling limit become greater than zero, assuming the character occurs in 20 percent of the population, (Simpson, Roe, and Lewontin; 1960). The value of 20 percent is a conservative approximation of the observed 18 percent. In no case in the counties discussed above were sample sizes greater than four.

I feel it is hazardous to draw any conclusion other than that the present samples from these counties are inadequate to provide even a basis for an intelligent guess as to validity in stating that the striped phenotype does not occur in these counties.

The distribution of the striped morph does not appear to be clinal, within the state. The Chisago County population has very nearly the same gene frequency as populations from the Itasca Park region although 150 miles separates the two areas. The stripe gene frequency in Marshall and Beltrami Counties is twice that calculated for the Itasca Park area. Perhaps if samples from areas between these widely separated localities were available, a gradual southeast-northwest increase might be revealed.

Since significant differences were found among counties, probably pooled state averages are not particularly useful in interpreting the ecology of this polymorphism in Rana sylvatica.

Since the results of the 1967 study of the five collection sites in the Itasca area indicated that significant seasonal differences do not occur and that gene frequencies are fairly stable over periods of five to eight years, there is an implication that selection pressures may be fairly constant. At least it is not apparent that selection changes seasonally.

In the Bog D population in the past few years there may have been a shift in selection value in favor of the stripe gene. It may have been in response to a change in microclimatic environment affecting some physiological component of the frog's constitution. Alternatively, theremay have been an increased advantage in this area of possessing the striped pattern, i.e., disruptive patterning may have become somewhat more advantageous. Since 1964, the striped morph has increased annually by 1 gene for every 100 of its nonstriped alleles.

Perhaps the shift might be attributed to the immigration and emigration of animals in the area. One would expect that the selective forces acting on the resident population would act in the same

manner on the new arrivals unless, of course, the factor promoting the immigration was itself the selecting force, e.g., drought.

The increase could also be a reflection of the collection method. It is true that collections were made by groups of four or more people but this was also true of Mary Creek collections as well as some of the Campground Pond collections. Furthermore, the 1964 and 1965 collections were made by different groups of people, which reduces the possibility that the collectors were selecting striped animals. To avoid the introduction of unnecessary bias during collection, an attempt was made to follow and capture individual frogs regardless of phenotype.

It has been assumed that selection acted primarily on adult woodfrogs, which could very well be an erroneous assumption, inasmuch as the larvae may come under selection pressures of the same sort and magnitude as the adults or possibly under an entirely different group of selective pressures. There was no significant differences between larval and resident frog frequencies, suggesting that selection does not seem to be operating between the time of the onset of metamorphosis and emergence from the ponds.

In only one instance was the larval stripe frequency greatly different from that of the resident population (Wood Pond) and this was not significant,

(Table 20b).

The Long Pond larval stripe frequency in 1966 was slightly higher that the resident frog population but not significantly so (Table 20a).

Young-of-the-year from the Campground Chain Ponds and Wegmann's Pond had slightly lower frequencies than the resident populations around these ponds, however they were not significantly different (Table 21a and b).

Samples of young-of-the-year taken from Icehouse Pond in 1964 exhibited a slightly higher frequency than the resident frequencies calculated for other years.

There is an inherent difficulty in assessing selection in regard to the stripe gene in the larva in that the gene's expression is not evident until the onset of metamorphosis. The dorsal stripe appears at about the same time as the front limbs become evident. Prior to its appearance there is no visible means of distinguishing the phenotypes. Therefore, any differences in behavior or developmental factors are not accessible. Differential mortality at metamorphosis may be a factor, although when frogs completed metamorphosis under laboratory conditions, the two phenotypes appeared to be equally viable (Browder et al. 1966).

Common to the maintenance of most polymorphisms

that have been investigated has been the manifestation of hybrid vigor. Heterosis may play a part in the woodfrog polymorphism as well, although there is no evidence for its being involved.

An unexpected discovery during the 1967 summer study of several ponds was the difference in age class structure in the two different habitat types involved in the study. Ponds in primarily coniferous habitats were populated by significantly higher numbers of juvenile frogs than ponds in mixed woods. The two areas classified as coniferous habitat, Mary Creek and Bog D Trail Pond, have extensive areas of moss, Sphagnum sp., in which juvenile frogs were especially abundant. Perhaps the moss provides more effective escape cover for the smaller frogs. Escape cover in mixed forest areas consisted of sparse vegetation and forest floor litter. Ponds in mixed habitats, Campground Pond, Campground Chain Ponds, and La Salle Pond were characteristically temporary, hence more xeric around their margins. These ponds were typical upland ponds situated on slope drainages and therefore surrounded by well drained terrain where Sphagnum is rare.

The summer of 1967 was most unusual; in June there was excessive rainfall, 4.01 inches above the average. In July rain was exceedingly scant (.29 inches), 3.29 inches below the normal; consequently the drainage ponds (mixed forest areas) were dry by the latter part

of July, shortly after metamorphosis of the year's larvae. After another month of scant moisture (.86 inches), 2.64 inches below the average, frogs were notably scarce in August around these ponds, particularly resident animals. Young-of-the-year were the most numerous, possibly due to limited dispersal of the young-of-the-year.

Under the prevailing drought conditions adult animals may have emigrated from the ponds due to their drying. Pond desiccation undoubtedly reduced the amount of food available to the frogs. The feeding efficiency of a sizable woodfrog around a drying pond may be reduced considerably because the time involved in searching for and capturing of food items may be too great for the benefit realized. Young-of-the-year, however, might be able to maintain themselves adequately on available food in such areas. A definite decrease in adult mosquito numbers was evident as might be expected.

Due to their unfavorable surface/volume ratios, the young-of-the-year may have been prevented from leaving the pond sites even though the ponds were drying. It may have been necessary to make an extensive terrestrial trip during a period of "desert-like" conditions for these small frogs. Apparently, humidity may play a role in frog movement (Bellis 1962).

There exists the possibility that the sample taken from Campground Pond in August, consisting solely of juveniles was not representative of the existing population. It was taken shortly before noon on a cloudy day and it was cool with a high of 72° F. However, on July 29 a sample of 14 frogs taken from the same pond consisted of 71 percent juveniles. This sample was collected during the afternoon and the high temperature for the day was 80° F. The pond at this time was fairly dry with no standing water but was muddy at the deepest spots. This suggests that perhaps the time of collection may not be as important as thought.

Mary Creek, in the latter part of August, still contained running water. The extensive sphagnum area, previously mentioned, was very moist, probably due to springs in the area. The majority of the frogs taken at this time were collected in this area. Bog D Trail Pond, in the sphagnum area was very moist as well, with some standing water and frogs were extremely abundant here.

To explain the paucity of animals, especially resident frogs, in August around the dried ponds is not particularly difficult. Emigration from the area apparently was responsible for the scarcity resulting in an inadequate sample at that time. A combined total for the three mixed forest habitat ponds in

August was 16 animals as compared to 184 for the coniferous habitat. Whether the frogs from dried ponds migrated to the more mesic habitats is unknown. A Lincoln-Petersen Index population estimate for the Bog D Trail Pond in August was 15,753 frogs as the result of 1 recapture of 177 marked frogs. Previous estimates had indicated a population of approximately 850 (Table 24). The August estimate may indicate a very heavy mortality since only one of the marked animals was recaptured, or the presence of an enormous number of frogs in an area which once supported approximately 1/20th that many animals. There may have been considerable immigration between the mark and recapture periods. At this time of the year an influx into the area may also indicate grouping preparatory to hibernation.

SUMMARY

BREEDING BEHAVIOR

1. Breeding of northern Minnesota woodfrogs is highly dependent upon weather conditions. The length of the season may range from a week or less to several weeks.
2. Male breeding behavior is characterized by constant interaction among breeding chorus members.
3. Heterosexual encounters were most commonly brief and ended successfully in amplexus.
4. Mated pairs were often observed at the pond's edge suggesting that the females are captured shortly after they enter the pond.
5. Oviposition is brief and accomplished in a head-down position. The eggs are usually attached to sedges or grass stems.
6. If a bush or tree is available in the pond, egg masses are deposited near their bases.
7. Egg masses are deposited in groups of 20 to 200.
8. Multiple amplexi are observed when breeding choruses become large.

LARVAL GROWTH

1. Larvae from two ponds in Itasca State Park

exhibited unlike growth rates in certain body dimensions.

2. Long Pond animals were significantly heavier in dry and ash weight, the latter throughout the study.
3. Low mineral content in coniferous forest soils was suggested as the possible cause of the smaller and lighter tadpoles in Wood Pond. Hind limbs were significantly longer on tadpoles from Long Pond.
4. High pond temperatures and drought were probably contributory factors for the hastened metamorphosis in Wood Pond.
5. Body water contents were very similar for larvae from both ponds throughout the study.
6. Weight loss exhibited by the larvae at metamorphosis was approximately 95 percent water.
7. Labial tooth rows seem to increase with age and/or length.
8. Tooth rows were extremely variable, encompassing the Rana pipiens formulae in early samples.
9. Wood Pond tadpoles had more constant tooth formulae than those in Long Pond.
10. Multiple breeding sessions were suggested as the reason for the more heterogeneous samples from Long Pond.

STRIPE POLYMORPHISM

1. A statewide stripe frequency of 17.6 percent was calculated.
2. County frequencies ranged from 15.2 to 32 percent, the differences among them were significant.
3. The higher frequencies occurred in northwestern Minnesota.
4. Differences in frequencies of the stripe phenotype among ponds in Itasca State Park were not significant.
5. No seasonal shifts in the stripe frequency were detected among the populations sampled.
6. Martof and Humphries' (1959) distribution map of Minnesota is incorrect.
7. The stripe distribution does not appear to be clinal.
8. There do not appear to be significant changes in stripe frequency from year to year in Itasca State Park.
9. Collecting methods as affecting the Bog D population are discussed. Migration in relation to stripe frequency changes and age structure is examined.
10. The dorsal stripe becomes evident with the onset of climax metamorphosis, thereby limiting the study of selection to postmetamorphic and adult frogs.
11. Comparison of larval stripe frequencies with "resident" populations around the same pond

revealed no significant differences.

12. Newly metamorphosed frog frequencies were not significantly different from "resident" frog frequencies.
13. The stripe gene is found primarily in heterozygotes.
14. The age class structure of the populations in coniferous and mixed woods was different. Significantly higher numbers of juveniles were associated with the coniferous areas.
15. Sphagnum was thought to have provided a better escape cover for juveniles in the coniferous areas.
16. Drought conditions in late summer apparently caused an emigration of frogs from the mixed woods ponds.
17. Tadpole behavior was discussed.
18. A description of the woodfrog tadpole and its mouthparts was presented.

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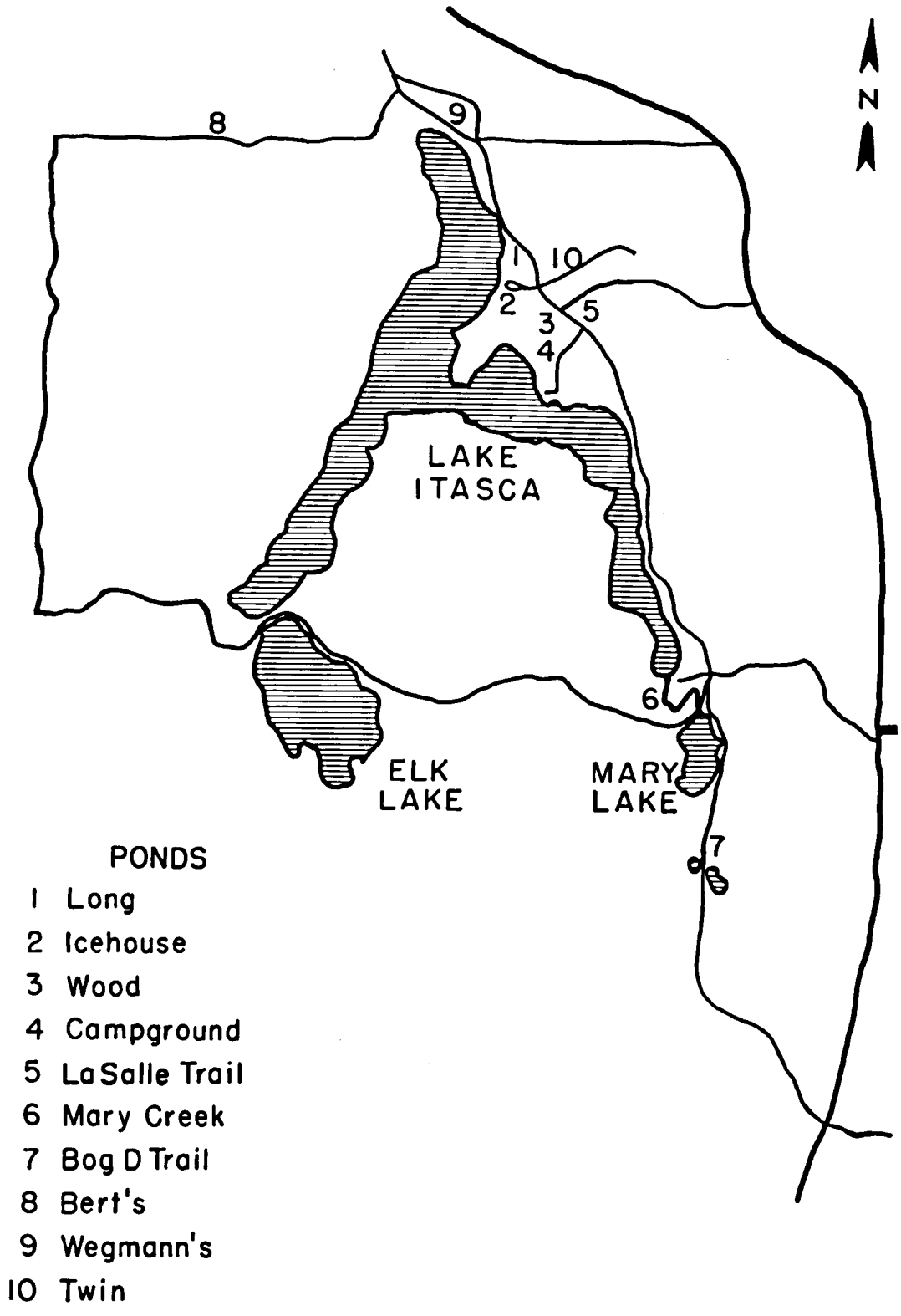


Figure 1. Itasca State Park map with woodfrog collection sites.

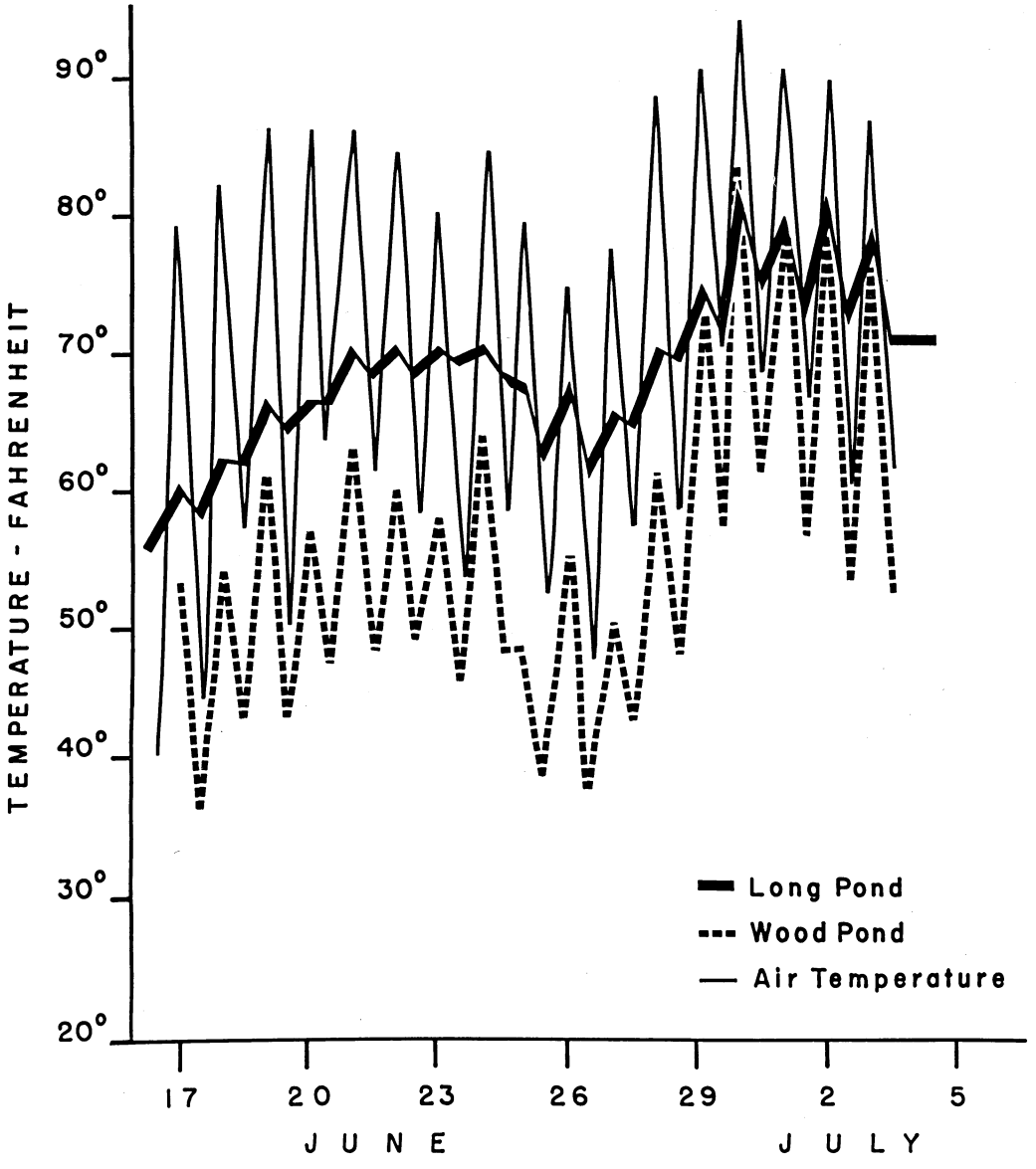


Figure 2. Pond and air temperature curves - daily high and low temperatures plotted.

Figure 3. Linear growth rate curves-means plotted.

TL - Total Length

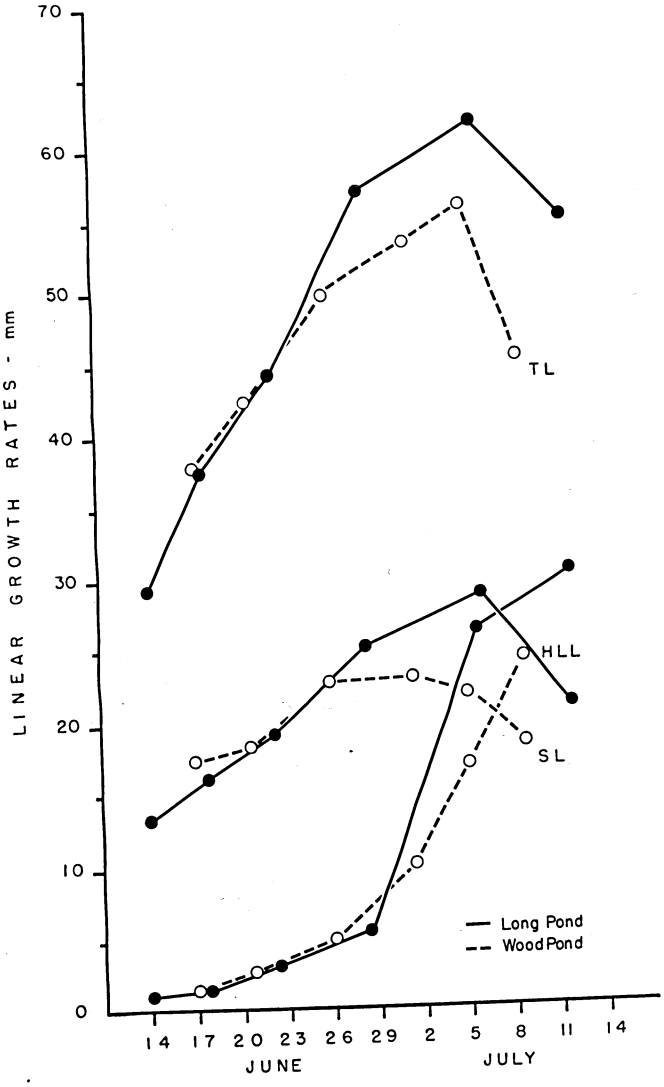
HLL - Hind Limb Length

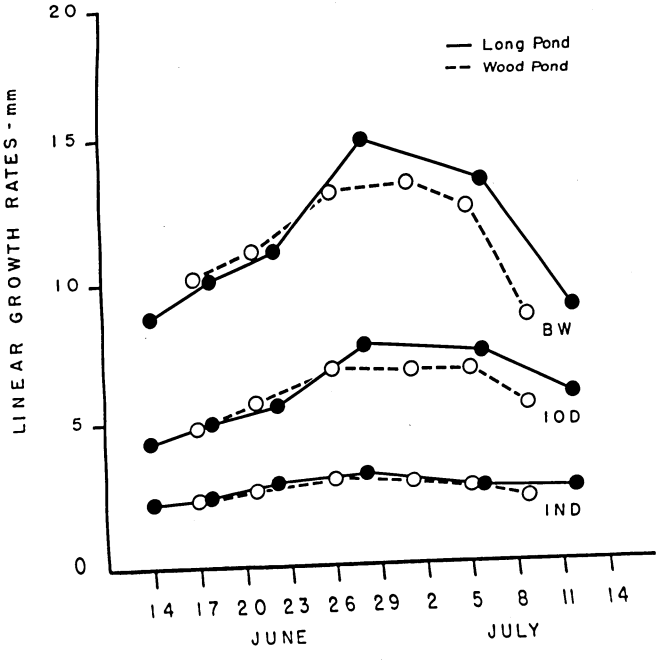
SL - Standard Length

BW - Body Width

IOD - Interorbital Distance

IND - Internaral Distance


LINEAR GROWTH RATES - mm
70
60
50
40
30
20
10
0
TL
HLL
SL
Long Pond
Wood Pond
14 17 20 23 26 29 2 5 8 11 14
JUNE
JULY


LINEAR GROWTH RATES - mm
20
15
10
5
0
Long Pond
Wood Pond
BW
IOD
IND
14 17 20 23 26 29 2 5 8 11 14
JUNE
JULY

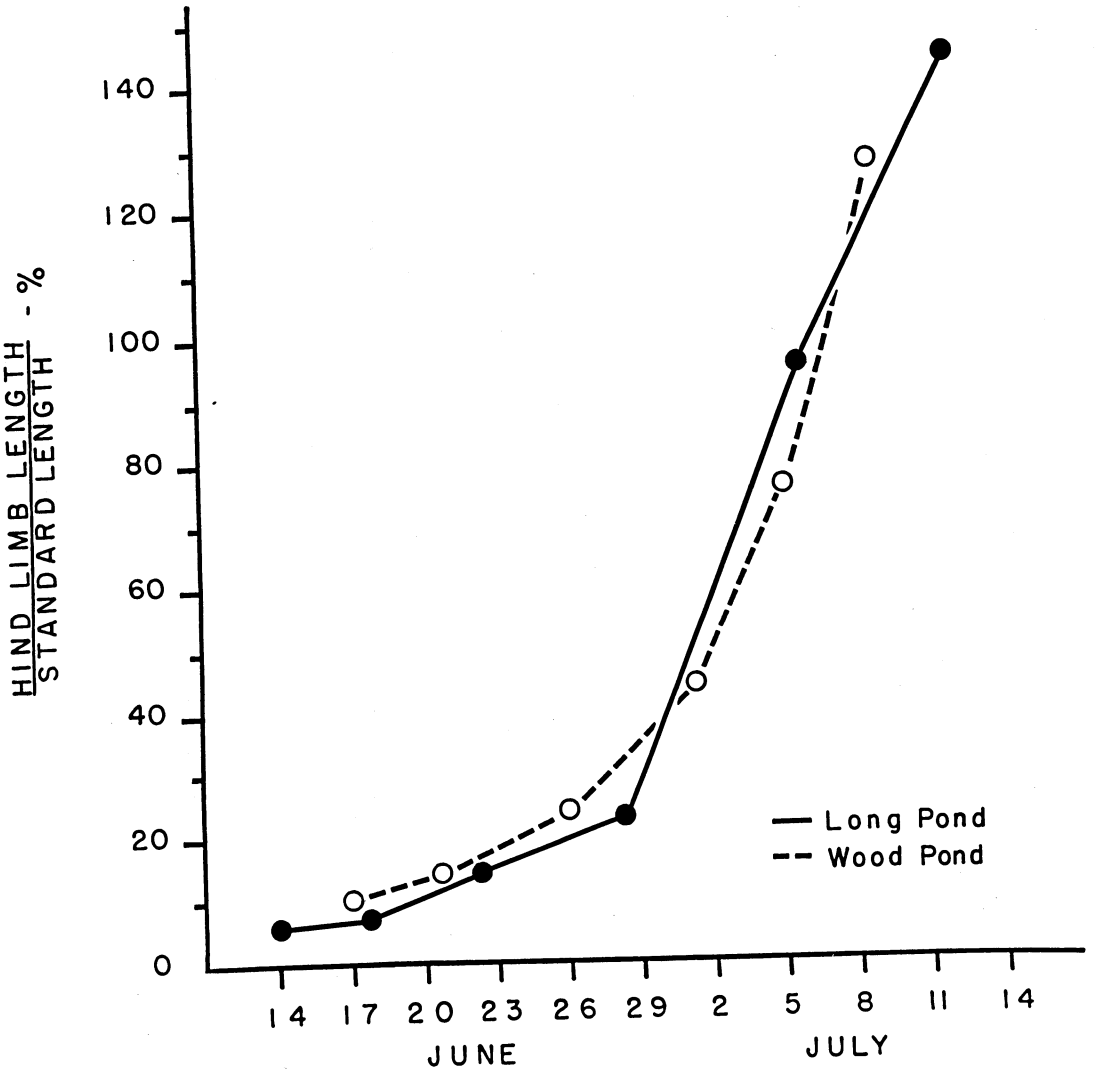
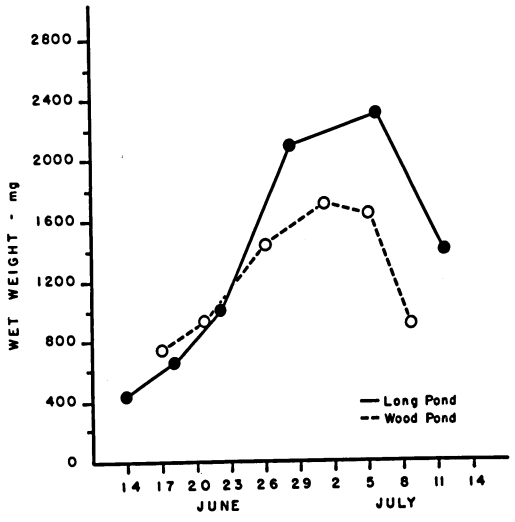
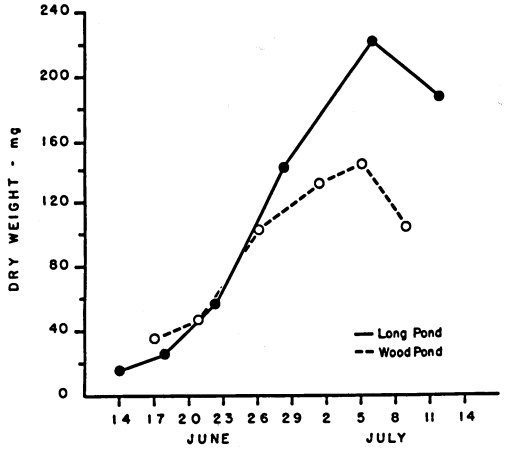
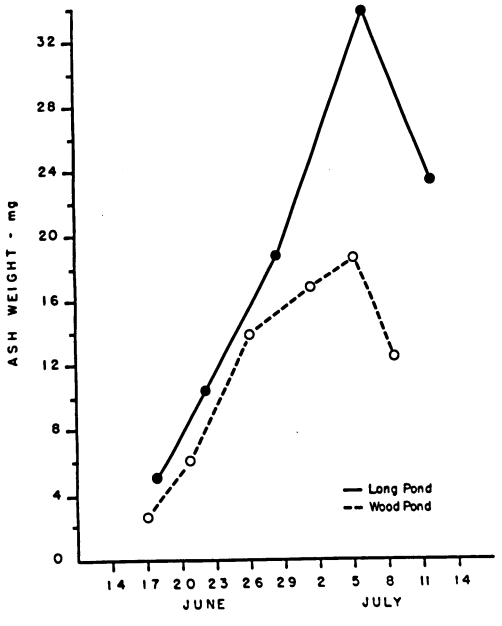


Figure 4. Hind limb length/standard length curves-means plotted.

Figure 5. Wet, dry and ash body weight curves-means plotted.


WET WEIGHT - mg
2800
2400
2000
1600
1200
800
400
0
14 17 20 23 26 29 2 5 8 11 14
JUNE
JULY
Long Pond
Wood Pond


DRY WEIGHT - mg
240
200
160
120
80
40
0
14 17 20 23 26 29 2 5 8 11 14
JUNE
JULY
Long Pond
Wood Pond


ASH WEIGHT - mg
32
28
24
20
16
12
8
4
0
14 17 20 23 26 29 2 5 8 11 14
JUNE
JULY
Long Pond
Wood Pond

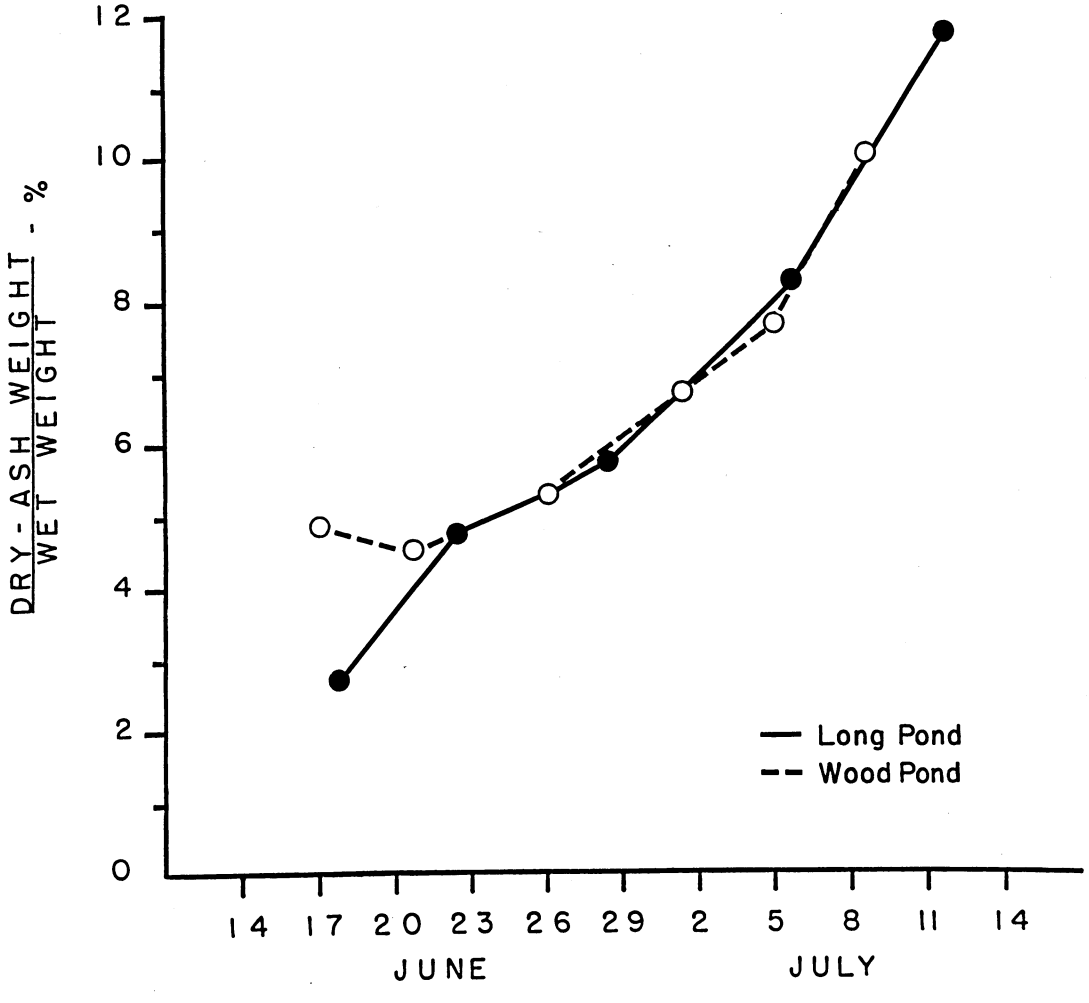
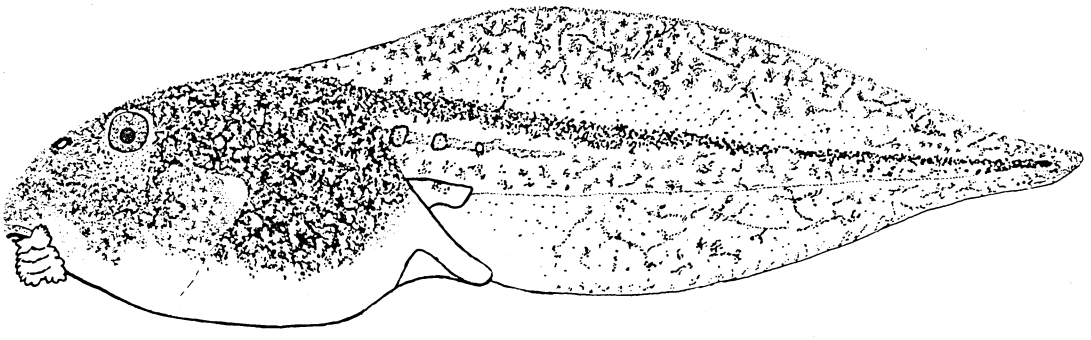
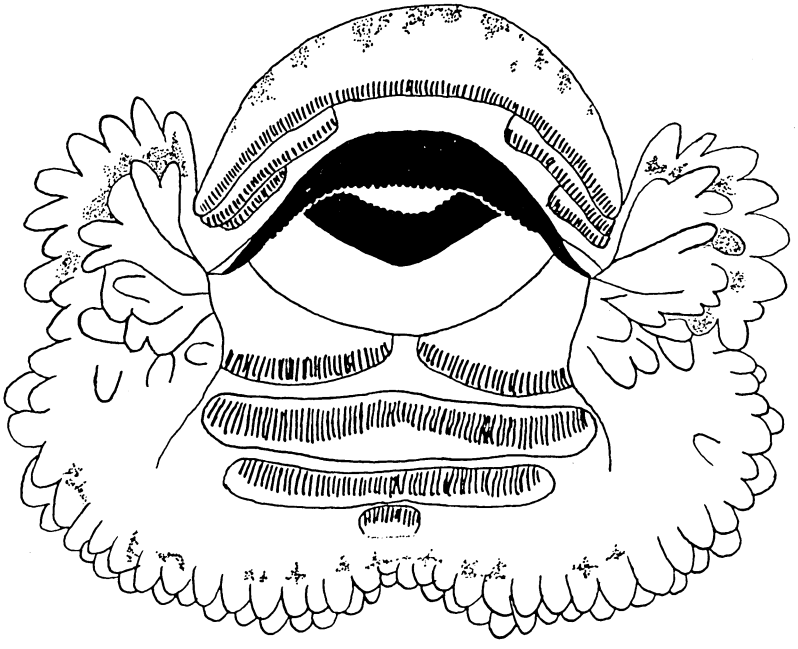


Figure 6. Dry weight/wet weight curves expressed as percent, means plotted.



Rana sylvatica tadpole x4.8.



Rana sylvatica tadpole mouthparts x5.

Figure 7.

Key to vegetation maps in Figures 8 - 12.

 - Aspen

 - Conifers

 - Grass

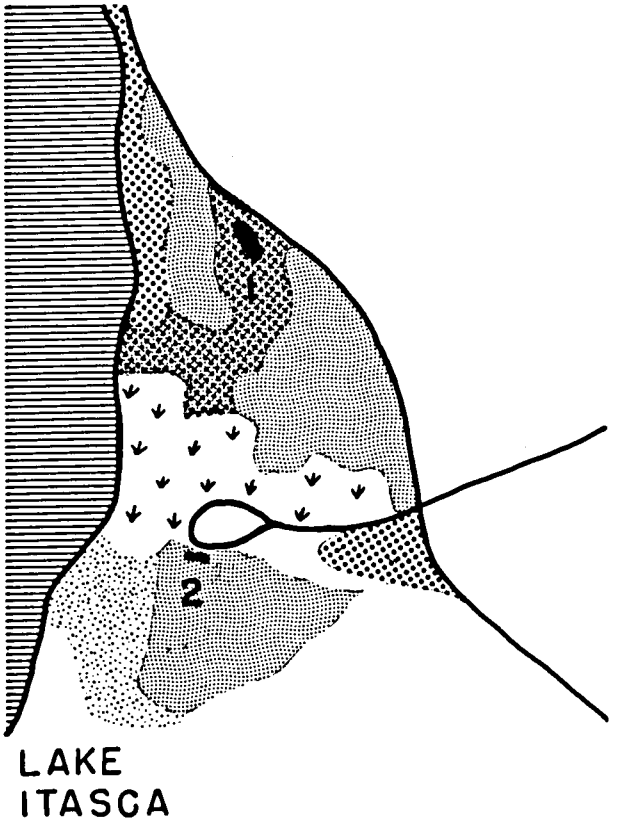
 - Upland Hardwoods

- Brush

- Shrub

Figure 8. (1) Long Pond; (2) Icehouse Pond.

Figure 9. (3) Wood Pond; (4) Campground and Campground Chain Ponds.


1
2
LAKE
ITASCA

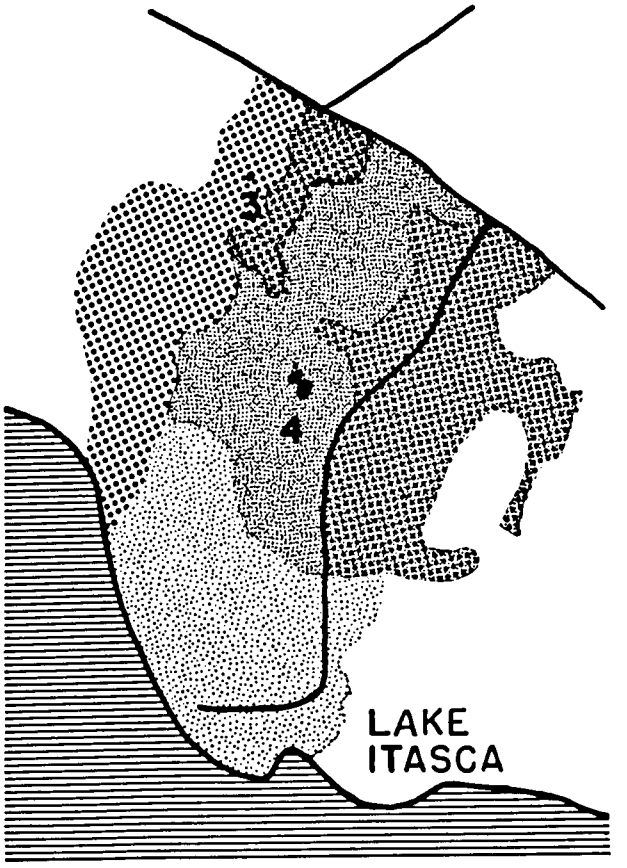

3
4
LAKE
ITASCA

Figure 10. (5) La Salle Pond.

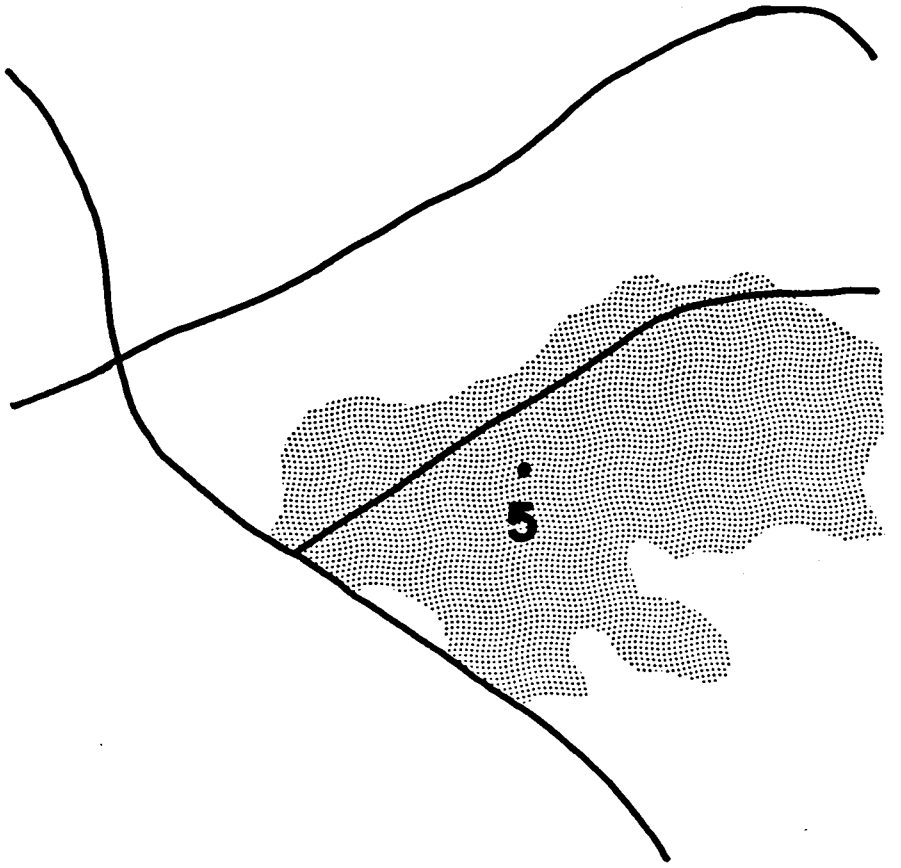
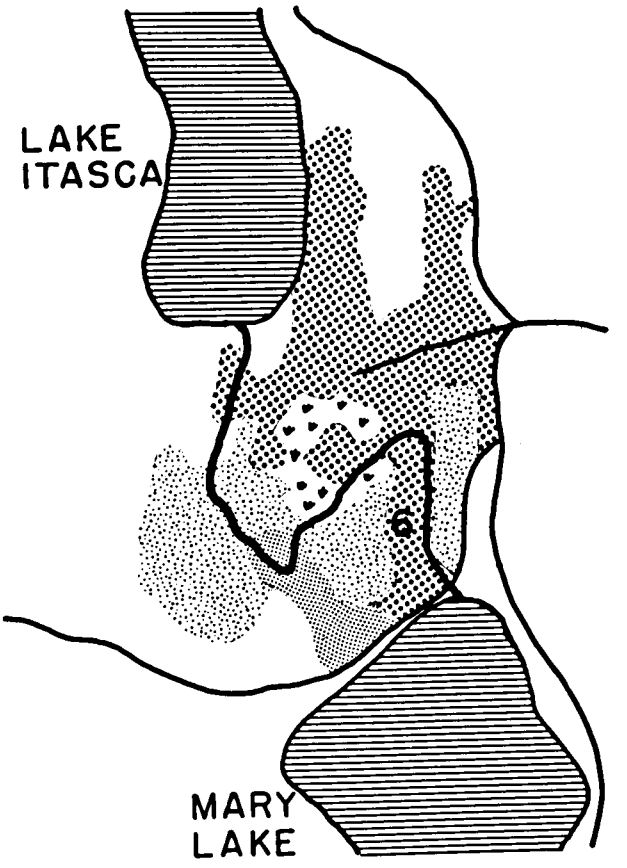
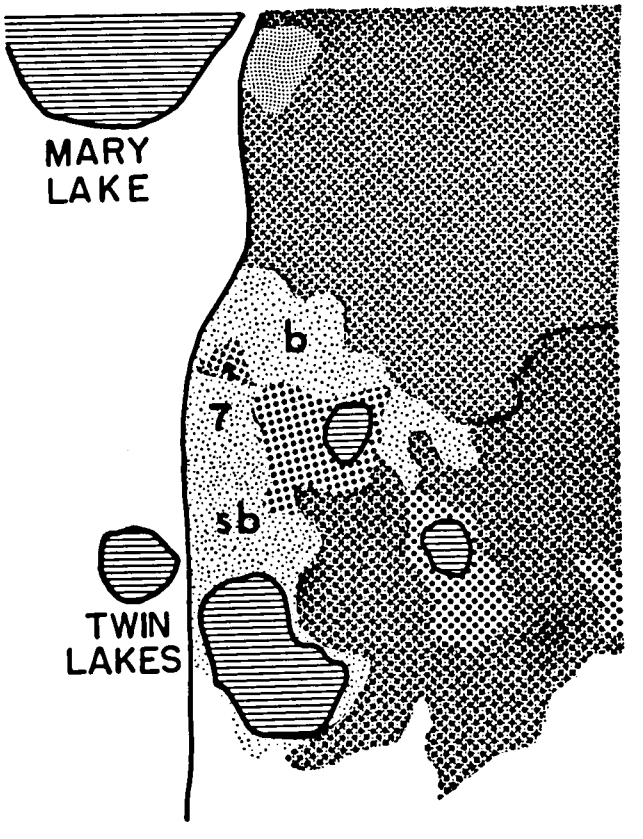

5

Figure 11. (6) Mary Creek.

Figure 12. (7) Bog D Trail Pond.


LAKE
ITASCA
6
MARY
LAKE


MARY
LAKE
b
7
sb
TWIN
LAKES

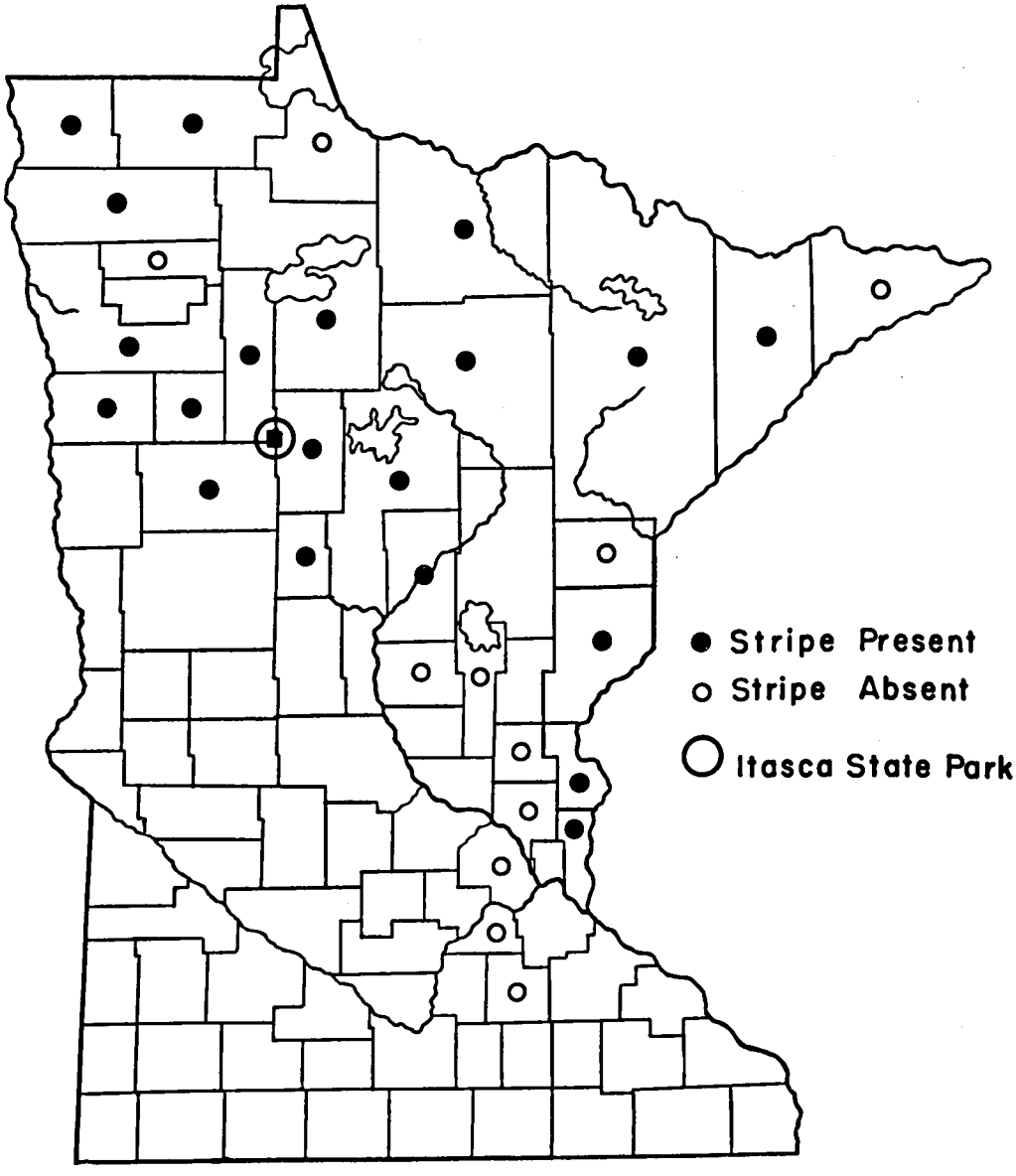


Figure 13. Distribution map of the occurrence of the woodfrog in Minnesota.

Figure 14. Age frequency histogram - juveniles are represented by animals 36 mm or less; adults 37 mm or greater.

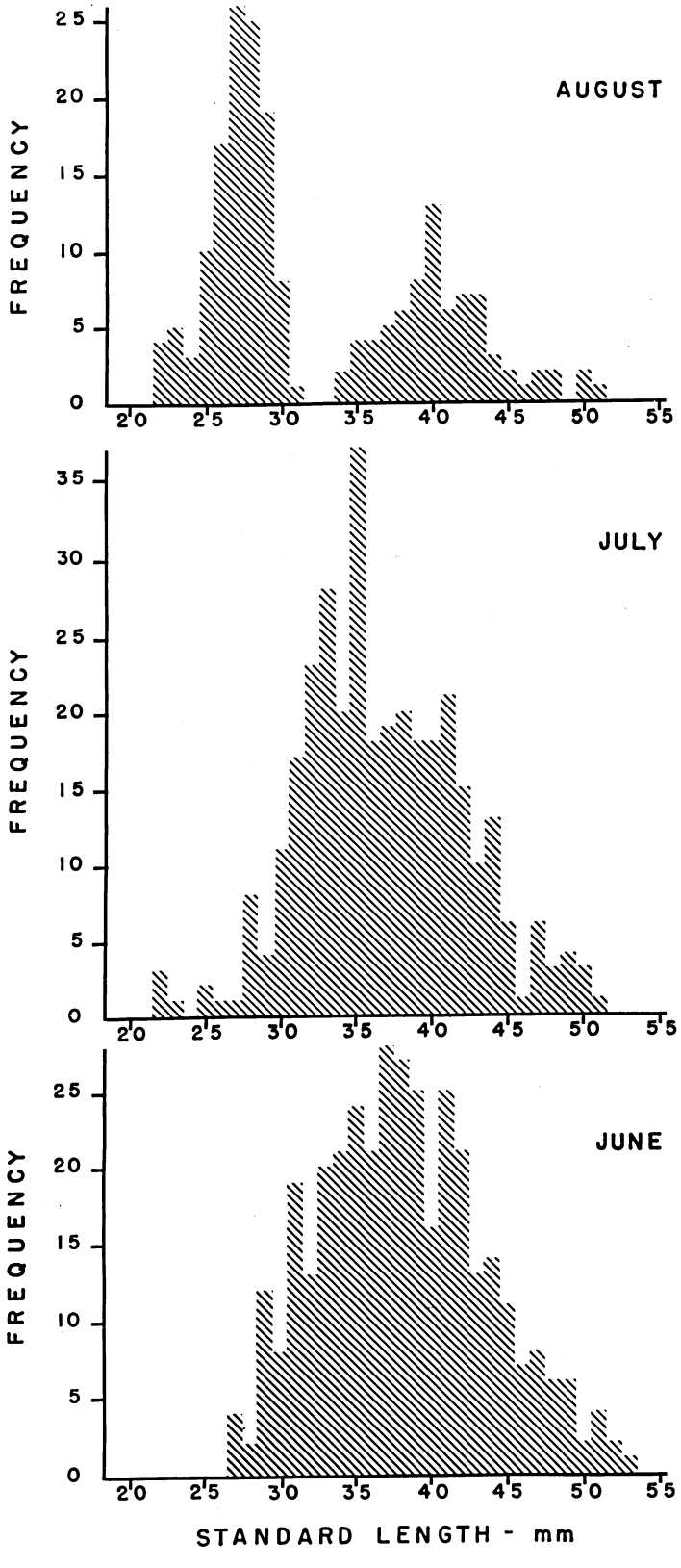

AUGUST
JULY
JUNE
FREQUENCY
FREQUENCY
FREQUENCY
0
5
10
15
20
25
30
35
2'0
2'5
3'0
3'5
4'0
4'5
5'0
5'5
STANDARD LENGTH - mm

TABLE 1. ANALYSIS OF VARIANCE (Long Pond)

(a) TOTAL LENGTH # = greater value

Date	Sample Size	MSA	MSW	F Value	Probability of Larger F	Significance
Week I - II#	38	.0507	.0025	20.280	p<.0005	**
Week II-III#	29	.0916	.0010	91.600	p<.0005	**
Week III-IV#	16	.0035	.0004	8.750	.005<p<.01	*
July 6# - 12	13	.0057	.0009	6.333	.025<p<.05	*

(b) STANDARD LENGTH

Week I - II#	38	.0457	.0022	20.773	p<.0005	**
Week II-III#	29	.0934	.0008	116.750	p<.0005	**
Week III-IV#	16	.0052	.0017	3.059	.10<p<.25	ns
July 6# - 12	16	.0390	.0017	22.941	p<.0005	**

Table 1. (continued)

(c) TAIL LENGTH # = greater value

Date	Sample Size	MSA	MSW	F Value	Probability of Larger F	Significance
Week I - II#	38	.0538	.0045	11.956	.001<p<.005	**
Week II-III#	29	.0930	.0027	34.444	p<.0005	**
Week III-IV#	16	.0014	.0014	1.000	.25<p<.50	ns
July 6 - 12#	13	.0001	.0027	0.0037	p<.995	ns

(d) TAIL HEIGHT

Week I - II#	38	.0087	.0006	14.500	p<.0005	**
Week II-III#	29	.0476	.0005	95.200	p<.0005	**
Week III#-IV	16	.0045	.0003	15.000	.001<p<.005	**
July 6 - 12	no measurements					

Table 1. (continued)

(e) INTERORBITAL DISTANCE # = greater value

Date	Sample Size	MSA	MSW	F Value	Probability of Larger F	Significance
Week I - II#	38	.0021	.00016	13.125	.0005<p<.001	**
Week II-III#	29	.0219	.00013	168.461	p<.0005	**
Week III#-IV	16	.0006	.00022	2.727	.10<p<.25	ns
July 6# - 12	16	.0024	.0002	12.000	.001<p<.005	**

(f) INTERNARAL DISTANCE

Week I - II#	38	.0013	.00004	32.500	p<.0005	**
Week II-III#	29	.0011	.00003	36.667	p<.0005	**
Week III#-IV	16	.0010	.00001	100.000	p<.0005	**
July 6# - 12	16	0	0		p=1	ns

Table 1. (continued)

(g) HIND LIMB LENGTH # = greater value

Date	Sample Size	MSA	MSW	F Value	Probability of Larger F	Significance
Week I - II#	38	.0197	.0003	65.667	p<.0005	**
Week II-III#	29	.0622	.0005	124.400	p<.0005	**
Week III-IV#	16	.3843	.0014	274.500	p<.0005	**
July 6 - 12#	16	.0185	.0022	8.409	.01<p<.025	*

(h) WET WEIGHT

Week I - II#	33	.0496	.0026	19.077	p<.0005	**
Week II-III#	24	.2253	.0017	132.529	p<.0005	**
Week III-IV#	16	.0019	.0019	1.000	.25<p<.50	ns
July 6# -12	13	.3823	.0040	95.575	p<.0005	**

Table 1. (continued)

(i) DRY WEIGHT # = greater value

Date	Sample Size	MSA	MSW	F Value	Probability of Larger F	Significance
Week I - II#	35	.0017	.00002	85.000	p<.0005	**
Week II-III#	17	.0027	.00003	90.000	p<.0005	**
Week III-IV#	7	.0016	.0001	16.000	.01<p<.025	*
July 6# - 12	13	.0005	.00015	3.333	.05<p<.10	ns

(j) ASH WEIGHT

Week I - II#	34	.000038	.000001	38.000	p<.0005	**
Week II-III#	25	.000074	.000002	37.000	p<.0005	**
Week III-IV#	16	.000123	.000002	61.500	p<.0005	**
July 6# - 12	13	.000055	.000001	30.556	p<.0005	**

Table 2. ANALYSIS OF VARIANCE (Wood Pond)

(a) TOTAL LENGTH # = greater value

Date	Sample Size	MSA	MSW	F Value	Probability of Larger F	Significance
Week I - II#	30	.0142	.0031	14.581	.025<p<.05	*
Week II-III#	32	.0368	.0029	12.690	.001<p<.005	**
Week III-IV#	26	.0180	.0012	15.000	.0005<p<.001	**
July 5# - 9	18	1.1623	.0012	968.583	p<.0005	**
(b) STANDARD LENGTH						
Week I - II#	30	.0067	.0026	2.577	.10<p<.25	ns
Week II-III#	32	.0558	.0026	21.462	p<.0005	**
Week III#-IV	26	.0005	.0007	0.714	.25<p<.50	ns
July 5# - 9	18	.0102	.0005	20.400	p<.0005	**

Table 2. (continued)

(c) TAIL LENGTH # = greater value

Date	Sample Size	MSA	MSW	F Value	Probability of Larger F	Significance
Week I - II#	30	.0206	.0049	4.204	.025<p<.05	*
Week II-III#	32	.0254	.0048	5.292	.025<p<.05	*
Week III-IV#	26	.0612	.0032	19.125	p<.0005	**
July 5# - 9	18	.0288	.0035	8.229	.01<p<.025	*

(d) TAIL HEIGHT

Week I - II#	30	.0053	.0008	6.625	.01<p<.025	*
Week II-III#	32	.0096	.0008	12.000	.001<p<.005	**
Week III#-IV	26	.0004	.0008	0.500	.25<p<.50	ns
July 5 - 9	no measurements					

Table 2. (continued)

(e) INTERORBITAL DISTANCE # = greater value

Date	Sample Size	MSA	MSW	F Value	Probability of Larger F	Significance
Week I - II#	30	.0037	.0004	9.250	.001<p<.005	**
Week II-III#	32	.0072	.0003	24.000	p<.0005	**
Week III#-IV	26	0	.00016	0	p=1	ns
July 5# - 9	18	.0037	.00019	19.474	.0005<p<.001	**

(f) INTERNARAL DISTANCE

Week I - II#	30	.0008	.00008	10.000	.001<p<.005	**
Week II-III#	32	.0005	.00003	16.667	p<.0005	**
Week III#-IV	26	.0007	.00006	11.667	.001<p<.005	**
July 5# - 9	18	.0005	.00008	6.250	.01<p<.025	*

Table 2. (continued)

(g) HIND LIMB LENGTH						# = greater value
Date	Sample Size	MSA	MSW	F Value	Probability of Larger F	Significance
Week I - II#	30	.0039	.0003	13.000	.001<p<.005	**
Week II-III#	32	.0536	.0007	76.571	p<.0005	**
Week III-IV#	26	.3526	.0057	61.859	p<.0005	**
July 5 -9#	18	.0030	.0079	0.380	.25<p<.50	ns
(h) WET WEIGHT						
Week I - II#	28	.0087	.0045	1.933	.05<p<.10	ns
Week II-III#	32	.0809	.0042	19.262	p<.0005	**
Week III-IV#	26	.0090	.0020	4.500	.025<p<.05	*
July 5# - 9	18	.0533	.0023	23.174	p<.0005	**

Table 2. (continued)

(i) DRY WEIGHT # = greater value

Date	Sample Size	MSA	MSW	F Value	Probability of Larger F	Significance
Week I - II#	28	0	.000046	0	p=1	ns
Week II-III#	31	.0021	.00006	35.000	p<.0005	**
Week III-IV#	25	.0026	.0001	26.000	p<.0005	**
July 5# - 9	18	.0007	.0001	7.000	.01<p<.025	*

(j) ASH WEIGHT

Week I - II#	27	.000012	.0000012	10.000	.001<p<.005	**
Week II-III#	30	.000074	.000002	37.000	p<.0005	**
Week III-IV#	25	.000025	.000003	8.333	.005<p<.01	**
July 5# - 9	18	.000018	.000004	4.500	p<.05	*

Table 3. ANALYSIS OF VARIANCE (Comparison of Ponds)

(a) LONG POND WOOD POND TOTAL LENGTH

Date	Sample Size	Date	Sample Size	MSA	MSW	F Value	Probability of larger F	Signif-icance	Pond with greater average
Wk I (June 18)	21	Wk I (June 17)	9	.0005	.0027	0.019	.999<p<.9995	ns	
Wk II (June 22)	17	Wk II (June 21)	21	.0027	.0028	0.964	.25<p<.50	ns	
Wk III (June 28)	12	Wk III (June 26)	11	.0206	.00059	34.915	p<.0005	**	LP
Wk IV (July 6)	4	Wk IV (July 5)	15	.0051	.0012	4.250	.05<p<.10	ns	

Table 3. (continued)

(b) LONG POND Date	Sample Size	WOOD POND Date	Sample Size	MSA	MSW	F Value	Probability of larger F	Signif-icance	Pond with greater average
				STANDARD LENGTH					
Wk I	21	Wk I	9	.0018	.0023	0.783	.25<p<.50	ns	
Wk II	17	Wk II	21	.0038	.0024	1.583	.10<p<.25	ns	
Wk III	12	Wk III	11	.0130	.00063	20.635	p<.0005	**	LP
Wk IV	4	Wk IV	15	.0302	.0016	18.875	.0005<p<.001	**	LP
(c)					TAIL LENGTH				
Wk I	21	Wk I	9	0	.0041	0	p=1	ns	
Wk II	17	Wk II	21	.0022	.0051	0.431	.25<p<.50	ns	
Wk III	12	Wk III	11	.0289	.0016	18.063	p<.0005	**	LP
Wk IV	4	Wk IV	15	.0002	.0037	0.00005	p>.9995	ns	

Table 3. (continued)

(d) TAIL HEIGHT

Date	Sample Size	Date	Sample Size	MSA	MSW	F Value	Probability of larger F	Signif-icance	Pond with greater average
	LONG POND		WOOD POND						
Wk I	21	Wk I	9	.0004	.0005	0.800	.25<p<.50	ns	
Wk II	17	Wk II	21	.0006	.0008	0.750	.25<p<.50	ns	
Wk III	12	Wk III	11	.0085	.0004	22.973	p<.0005	**	LP
Wk IV	4	Wk IV	15	.0003	.0009	0.333	.50<p<.75	ns	

(e) INTERORBITAL DISTANCE

Wk I	21	Wk I	9	.0001	.0002	0.500	.25<p<.50	ns	
Wk II	17	Wk II	21	.0003	.0003	1.000	.25<p<.50	ns	
Wk III	12	Wk III	11	.0020	.0001	20.000	p<.0005	**	LP
Wk IV	4	Wk IV	15	.0002	.0002	1.000	.25<p<.50	ns	

Table 3. (continued)

(f) LONG POND		WOOD POND		INTERNARAL DISTANCE					
Date	Sample Size	Date	Sample Size	MSA	MSW	F Value	Probability of larger F	Signif-icance	Pond with greater average
Wk I	21	Wk I	9	0	.000075	0	p=1	ns	
Wk II	17	Wk II	21	.0001	.00004	2.500	.10<p<.25	ns	
Wk III	12	Wk III	11	.0003	.00001	30.000	p<.0005	**	LP
Wk IV	4	Wk IV	15	0	.000071	0	p=1	ns	
(g)				HIND LIMB LENGTH					
Wk I	21	Wk I	9	.0002	.0002	1.000	.25<p<.50	ns	
Wk II	17	Wk II	21	.0022	.0004	5.641	.025<p<.05	*	LP
Wk III	12	Wk III	11	.0031	.0010	3.163	.05<p<.10	ns	
Wk IV	4	Wk IV	15	.0669	.0080	8.363	.01<p<.025	*	LP

Table 3. (continued)

(h) LONG POND WOOD POND — WET WEIGHT

Date	Sample Size	Date	Sample Size	MSA	MSW	F Value	Probability of larger F	Signif-icance	Pond with greater average
Wk I	21	Wk I	7	.0030	.0026	1.154	.25<p<.50	ns	
Wk II	12	Wk II	21	.0025	.0042	0.595	.25<p<.50	ns	
Wk III	12	Wk III	11	.0643	.0016	40.188	p<.0005	**	LP
Wk IV	4	Wk IV	15	.0275	.0024	11.458	.001<p<.005	**	LP

(i) DRY WEIGHT

Wk I	21	Wk I	7	.0002	.00002	10.000	.001<p<.005	**	WP
Wk II	14	Wk II	21	.0002	.000045	4.444	.025<p<.05	*	LP
Wk III	3	Wk III	10	.0009	.00005	18.000	.001<p<.005	**	LP
Wk IV	4	Wk IV	15	.0027	.00015	18.000	.001<p<.0005	**	LP

Table 3. (continued)

(j) LONG POND WOOD POND ASH WEIGHT

Date	Sample Size	Date	Sample Size	MSA	MSW	F Value	Probability of larger F	Signif-icance	Pond with greater average
Wk I	21	Wk I	7	.000009	.0000009	10.000	.001<p<.005	**	LP
Wk II	13	Wk II	20	.000028	.0000017	16.471	p<.0005	**	LP
Wk III	12	Wk III	10	.000022	.0000023	9.565	.005<p<.01	**	LP
Wk IV	4	Wk IV	15	.000125	.000004	312.500	p<.0005	**	LP

Table 4. Standard Length/Total Length Ratio (SL/TL)

		Long Pond		Wood Pond
	May 22	44.89		
	May 28	42.54		
	June 14	47.28		
Wk I	June 18	44.08	June 17	44.96
Wk II	June 22	43.84	June 21	43.38
Wk III	June 28	44.01	June 26	45.16
			July 1	41.96
Wk IV	July 6	45.28	July 5	39.04
	July 12	38.11	July 9	41.63
Mean = 44.56 (May 22 through July 6)			Mean = 43.86 (June 17 through July 1)	

Table 5. Standard Length/Body Width Ratio (SL/BW)

		Long Pond		Wood Pond
	May 28	1.62		
	June 14	1.64		
Wk I	June 18	1.64	June 17	1.66
Wk II	June 22	1.72	June 21	1.66
Wk III	June 28	1.72	June 26	1.72
			July 1	1.72
Wk IV	July 6	2.10	July 5	1.82
	July 12	2.35	July 9	2.23
Mean = 1.67 (May 28 through June 28)			Mean = 1.69 (June 17 through July 1)	

Table 6. Standard Length/Body Depth Ratio (SL/BD)

		Long Pond		Wood Pond
	May 22	2.44		
	28	2.19		
	June 14	2.17		
Wk I	18	2.34	June 17	2.35
Wk II	22	2.34	21	2.27
Wk III	28	2.40	26	2.36
			July 1	2.31
Wk IV	July 6	3.39	5	2.58
	Mean = 2.31		Mean = 2.32	
	(May 22 through June 28)		(June 17 through July 1)	

Table 7. Hind Limb/Standard Length Ratio (HL/SL) in Percent

		Long Pond		Wood Pond
	June 14	7.2		
Wk I	18	9.2	June 17	10.1
Wk II	22	14.6	21	13.0
Wk III	28	23.5	26	22.7
			July 1	44.0
Wk IV	July 6	95.0	5	75.0
	12	144.0	9	127.0

Table 8. Dry Matter (DM) and Water Content (WC) in percent of wet weight

	Long Pond			Wood Pond		
		DM	WC		DM	WC
Wk I	June 18	3.7	96.3	June 17	5.3	94.7
II	22	5.8	94.2	21	5.1	94.9
III	28	6.6	93.4	26	6.3	93.7
IV	July 6	9.7	90.3	July 5	8.8	91.2
	12	12.0	88.0	9	11.4	88.6

Table 9. Distribution of tooth formulae in tadpoles relative to time. Number in parentheses represents the number of animals per sample possessing each tooth formula.

WOOD POND

Date	Tooth Formulae 2/3	3/3	2/4	3/4	4/4	4/3	Sample Size
June 17	.09(1)	.36(4)	0	.55(6)	0	0	11
June 21	.05(1)	.40(9)	0	.55(12)	0	0	22
June 26	0	.36(4)	0	.55(6)	.09(1)	0	11
July 1	0	0	0	.70(9)	.15(2)	.15(2)	13
July 5	.08(1)	.15(2)	0	0	.46(6)	.31(4)	13
						TOTAL	70

LONG POND

Date	Tooth Formulae 2/3	3/3	2/4	3/4	4/4	4/3	Sample Size
June 14	.30(9)	.10(3)	.20(6)	.40(12)	0	0	30
June 18	.10(3)	.13(4)	.13(4)	.64(19)	0	0	30
June 22	0	.52(12)	0	.48(11)	0	0	23
June 28	0	.08(1)	0	.33(4)	.42(5)	.17(2)	12
July 6	0	0	0	.67(2)	.33(1)	0	3
						TOTAL	108

Table 10. Ash Weight/Wet Weight Ratio (Ash Wt./Wet Wt.) in percent

Wood Pond		Long Pond	
June 17	.33	June 18	.79
21	.64	22	.95
26	.96	28	.87
July 1	.97		
5	1.12	July 6	1.45
9	1.36	12	1.64

Table 11. List of Minnesota counties with frog totals collected from each.

County	Number of Frogs
Aitkin	0
Anoka	3
Becker	79
Beltrami	169
Benton	0
Big Stone	0
Blue Earth	0
Brown	0
Carlton	10
Carver	0
Cass	13
Chippewa	0
Chisago	66
Clay	0
Clearwater/Hubbard/ northeast Becker	4523
Cook	5
Cottonwood	0
Crow Wing	5
Dakota	0
Dodge	0
Douglas	0
Faribault	0
Fillmore	0
Freeborn	0
Goodhue	0
Grant	0
Hennepin	2
Houston	0
Isanti	4
Itasca	4
Jackson	0
Kanabec	0
Kandiyohi	0
Kittson	5
Koochiching	3
Lac Qui Parle	0
Lake	11
Lake of the Woods	5
Le Sueur	0
Lincoln	0
Lyon	0

Table 11. (continued)

County	Numbers of Frogs
Mahnomen	5
Marshall	95
Martin	0
McLeod	0
Meeker	0
Mille Lacs	1
Morrison	1
Mower	0
Murray	0
Nicollet	0
Nobles	0
Norman	3
Olmstead	0
Otter Tail	0
Pennington	2
Pine	12
Pipestone	0
Polk	6
Pope	0
Ramsey	0
Red Lake	0
Redwood	0
Renville	0
Rice	3
Rock	0
Roseau	3
St. Louis	13
Scott	3
Sherburne	0
Sibley	0
Stearns	0
Steele	0
Stevens	0
Swift	0
Todd	0
Traverse	0
Wabasha	0
Wadena	4
Waseca	0
Washington	3
Watonwan	0
Wilkin	0
Winona	0
Wright	0
Yellow Medicine	

Table 12. X^2 test for heterogeneity of stripe frequencies among samples taken from indicated counties.
S = Striped, NS = Nonstriped

County	Date	Phenotype Numbers S	NS	%S	X^2 Value	df	P/Sig.
Becker	1967	19	59	24.3	2.5152		
Beltrami	1958	53	113	32.0	23.7978		
Chisago	1960	10	56	15.2	.2585		
Itasca Area (Clearwater, Hubbard, Northeast Becker)	1964-1967	753	3770	16.7	2.4380		
Marshall	1958	27	57	32.0	23.7978		
		862	4055	17.6	52.8073	4	p<.005**

Table 13. X^2 test for heterogeneity of stripe frequencies among indicated months - data pooled from five areas sampled.
S = Striped, NS = Nonstriped

Month	Phenotype Numbers S	NS	%S	X^2 Value	df	P/Sig.
June	55	259	17.5	.8937		
July	88	330	21.1	.5322		
August	40	160	20.0	.0169		
	183	749	19.6	1.4428	2	.25<p<.50 ns

Table 14. X^2 test for heterogeneity of stripe frequencies between/among the indicated years in the following areas: S = Striped, NS = Nonstriped

(a) Mary Creek

Year	Phenotype S	Phenotype NS	%S	X^2 Value	df	P/ Sig.
1965	11	50	18.0			
1967	26	124	17.3			
	37	174		.0147	1	.90<p<.95 ns

(b) Bog D Trail Pond

Year	Phenotype S	Phenotype NS	%S	X^2 Value	df	P/ Sig.
1964	16	88	15.4			
1965	21	97	17.8			
1966	35	151	18.8			
1967	64	228	21.9			
	136	564	19.4	2.4875	3	.25<p<.50 ns

(c) Bog D Trail Pond

Year	Phenotype S	Phenotype NS	%S	X^2 Value	df	P/ Sig.
1964	16	88	15.4			
1967	64	228	21.9			
	80	316	20.2	.0010	1	.95<p<.975 ns

Table 14. (continued)

(d) La Salle Trail Pond

Year	Phenotype S	Phenotype NS	%S	X^2 Value	df	P/ Sig.
1961	23	128	15.2	.0173		
1964	6	17	26.1	1.5393		
1965	4	11	26.7	1.1288		
1967	13	77	17.8	.2728		
	46	233	16.5	2.9582	3	.25<p<.50 ns

(e) Icehouse Pond

Year	Phenotype S	Phenotype NS	%S	X^2 Value	df	P/ Sig.
1960	41	370	10.0	0.0000		
1964	19	180	9.5	.0395		
1966	5	39	11.4	.0952		
1967	1	7	12.5	.0571		
	66	596	10.0	.1918	3	.975<p<.990 ns

Table 15. X^2 test for heterogeneity of stripe frequencies between mixed/coniferous habitats - data pooled from five areas sampled.
S = Striped, NS = Nonstriped

Habitat	Phenotype Numbers S	NS	%S	X^2 Value	df	P/Sig.
Mixed	93	397	19.0			
Coniferous	90	352	20.4			
	183	749	19.6	.2814	1	.50<p<.75 ns

Table 16. X^2 test for heterogeneity of stripe frequencies between adults and juveniles in coniferous habitat for June, 1967. A = Adult, J = Juvenile

Phenotype	Age Class		%S		X^2 Value	df	P/ Sig.
	A	J	A	J			
Stripe	3	6	13.0	12.0			
Nonstripe	20	45					
	23	51			.0243	1	.75<p<.90 ns

July, 1967

Phenotype	Age Class		%S		X^2 Value	df	P/ Sig.
	A	J	A	J			
Stripe	8	36	20.5	24.8			
Nonstripe	31	109					
	39	145			.3145	1	.50<p<.75 ns

August, 1967

Phenotype	Age Class		%S		X^2 Value	df	P/ Sig.
	A	J	A	J			
Stripe	10	27	15.6	22.5			
Nonstripe	54	93					
	64	120			1.2280	1	.25<p<.50 ns

Table 16. (continued)
X^2 test for heterogeneity of stripe frequencies between adults and juveniles in mixed habitat for June, 1967.
A = Adult, J = Juvenile

Phenotype	Age Class A	J	%S A	J	X^2 Value	df	P/ Sig.
Stripe	32	14	19.2	19.2			
Nonstripe	135	59					
	167	73			0.0	1	p=1 ns

July, 1967

Phenotype	Age Class A	J	%S A	J	X^2 Value	df	P/ Sig.
Stripe	26	18	21.8	15.7			
Nonstripe	93	97					
	119	115			1.4708	1	.10<p<.25 ns

August, 1967

Phenotype	Age Class A	J	%S A	J	X^2 Value	df	P/ Sig.
Stripe	0	3					
Nonstripe	3	10					
	3	13			1.1475	1	.25<p<.50 ns

Table 17. X^2 test for heterogeneity of age structure between mixed and coniferous habitats for June through August.
A = Adult, J = Juvenile

Habitat	Age Class A	Age Class J	%J	X^2 Value	df	P/ Sig.
Mixed	289	201	41.0			
Coniferous	126	316	71.4			
	415	517		87.3615	1	p<.005 **

Table 18. X^2 test for heterogeneity of age structure between mixed and coniferous habitats for June, 1967.
A = Adult, J = Juvenile

Habitat	Age Class A	Age Class J	%J	X^2 Value	df	P/ Sig.	
Mixed	167	73	30.4				
Coniferous	23	51	69.0				
	190	124		350.8885	1	p<.005	**

July, 1967

Habitat	Age Class A	Age Class J	%J	X^2 Value	df	P/ Sig.	
Mixed	119	115	49.1				
Coniferous	39	145	78.8				
	158	260		38.5384	1	p<.005	**

August, 1967

Habitat	Age Class A	Age Class J	%J	X^2 Value	df	P/ Sig.	
Mixed	3	13	81.3				
Coniferous	64	120	65.2				
	67	133		1.6984	1	.10<p<.25	ns

Table 19. Gene frequencies for dates in areas listed.

Area	Year	f(S) = p	f(s) = q	n
Bog D Trail Pond	1964	.08	.92	104
	1965	.09	.91	118
	1966	.10	.90	186
	1967	.11	.89	292
Campground Pond	1967	.11	.89	175
Campground Chain Pond	1967	.11	.89	225
Icehouse Pond	1960	.05	.95	411
	1964	.05	.95	199
	1966	.06	.94	44
	1967	.06	.94	8
La Salle Trail Pond	1961	.08	.92	151
	1964	.14	.86	23
	1965	.14	.86	15
	1967	.07	.93	77
Mary Creek	1965	.09	.91	61
	1967	.09	.91	150
Becker County (Detroit Lakes)	1967	.14	.86	78
Beltrami County	1958	.18	.82	166
Chisago County	1960	.08	.92	66
Itasca Park Area (Hubbard and Clearwater Counties)	----	.09	.91	4523
Marshall County	1958	.18	.82	84
State of Minnesota	----	.09	.91	5057

Table 20. X^2 test for heterogeneity of stripe frequencies between larval and resident frogs for the areas indicated. S = Striped, NS = Nonstriped

(a) Long Pond

	Phenotype S	Phenotype NS	%S	X^2 Value	df	P/ Sig.
Larvae	4	18	18.2			
Resident	21	104	16.8			
				.0254	1	.75<p<.90 ns

(b) Wood Pond

	Phenotype S	Phenotype NS	%S	X^2 Value	df	P/ Sig.
Larvae	7	11	38.9			
Resident	5	15	25.0			
				.7403	1	.25<p<.50 ns

Table 21. X^2 test for heterogeneity of stripe frequencies between young-of-the-year and resident frogs for the areas indicated. S = Striped, NS = Nonstriped

(a) Campground Chain Ponds

	Phenotype S	Phenotype NS	%S	X^2 Value	df	P/ Sig.
Young-of-the-Year	15	74	16.8			
Resident	45	180	20.0			
				.4084	1	.50<p<.75 ns

(b) Wegmann's Pond

	Phenotype S	Phenotype NS	%S	X^2 Value	df	P/ Sig.
Young-of-the-Year	15	101	12.9			
Resident	14	71	16.4			
				.5007	1	.25<p<.50 ns

Table 22. X^2 test for heterogeneity between the stripe frequencies of suffocated frogs and the total sample from the indicated areas, June 30, 1967.
S = Striped, NS = Nonstriped

Area	Phenotype S	Phenotype NS	%S	X^2 Value	df	P/ Sig.
Campground Chain Ponds						
Suffocated Frogs	5	36	12.2			
Total Sample	16	59	21.3			
				1.4913	1	.10<p<.25 ns

Area	Phenotype S	Phenotype NS	%S	X^2 Value	df	P/ Sig.
La Salle Pond						
Suffocated Frogs	4	20	16.6			
Total Sample	8	28	22.2			
				.2778	1	.50<p<.75 ns

Table 23. List of probabilities of obtaining a sample of the indicated size containing no striped woodfrogs from the counties indicated.

County	Sample Size	Collection Date	Probability (0)
Anoka	1	(4/21/38)	.820
	2	(5/27/36)	.672
Carlton	3	(5/20/36)	.551
	2	(1937)	.672
	1	(7/27/38)	.820
	1	(7/6/48)	.820
	1	(7/9/48)	.820
	1	(8/27/58)	.820
	1	(8/22/59)	.820
Cook	2	(6/27/41)	.672
	3	(7/13/48)	.551
Hennepin	1	(8/24/52)	.820
	1	(7/12/38)	.820
Isanti	1	(5/30/55)	.820
	3	(summer 1953)	.551
Lake of the Woods	1	(8/21/49)	.820
	4	(6/27/55)	.452
Mille Lacs	1	(4/4/42)	.820
Morrison	1	(5/26/34)	.820
Pennington	2	(7/18/58)	.672
Rice	2	(5/13/38)	.672
	1	(5/15/38)	.820
Scott	3	(5/31/52)	.551

Table 24. Population estimate using the Lincoln-Petersen Index for dates and areas indicated.

Area	Date	Estimate
La Salle Trail Pond	June 29 – 30	$\frac{32}{x} = \frac{3}{18}$, $x = 192$
Bog D Trail Pond	May 28 – June 14	$\frac{125}{x} = \frac{10}{61}$, $x = 763$
	June 19 – July 6	$\frac{14}{x} = \frac{3}{184}$, $x = 859$
	July 6 – August 25	$\frac{177}{x} = \frac{1}{89}$, $x = 15{,}753$
Campground Pond	June 13, 22 – 30	$\frac{42}{x} = \frac{6}{49}$, $x = 343$
	June 30 – July 7	$\frac{85}{x} = \frac{14}{53}$, $x = 307$
	July 7 – 29	$\frac{124}{x} = \frac{4}{14}$, $x = 434$

APPENDIX I. LONG POND

Total Length (mm)

Date	Range	Mean	Standard Deviation	Sample Size
May 22	9.0-10.8	9.8	.6	12
28	10.4-16.7	13.6	1.6	24
June 14	18.5-36.7	29.4	5.0	19
18	30.0-46.7	37.2	5.0	21
22	34.8-48.5	43.8	3.7	17
28	50.8-60.8	56.8	2.5	12
July 6	57.6-64.1	61.4	2.8	4
12	47.8-61.7	55.4	4.1	9

Standard Length (mm)

May 22	3.8- 4.9	4.4	.3	12
28	4.3- 6.9	5.7	.7	26
June 14	9.4-16.6	13.9	1.9	21
18	12.5-20.0	16.4	2.1	21
22	16.3-21.4	19.2	1.4	17
28	23.3-27.1	25.0	1.2	12
July 6	22.4-35.0	27.8	5.3	4
12	19.4-22.5	21.1	1.0	12

Tail Height (mm)

May 22	2.2- 2.7	2.5	.1	12
28	2.4- 3.7	3.1	.4	25
June 14	5.2-10.1	8.3	1.2	21
18	8.0-12.0	9.6	1.1	21
22	8.0-13.3	11.0	1.2	17
28	13.5-16.4	15.4	.9	12
July 6	11.9-14.5	13.2	.1	4

APPENDIX I. (continued)

Body Width (mm)

Date	Range	Mean	Standard Deviation	Sample Size
May 22	1.5- 2.1	1.8	.2	12
28	2.9- 4.3	3.5	.4	26
June 14	6.3- 9.8	8.5	.9	21
18	8.5-11.6	10.0	1.1	21
22	10.0-13.0	11.1	.8	17
28	13.6-15.6	14.6	.7	12
July 6	10.7-15.0	13.2	2.1	4
12	7.0-10.4	9.0	1.1	12

Body Depth (mm)

May 22	1.7- 2.1	1.8	.1	12
28	1.5- 3.4	2.7	.4	26
June 14	4.7- 7.3	6.4	.8	21
18	5.7- 8.3	7.0	.7	21
22	7.1- 9.3	8.2	.5	17
28	9.5-11.3	10.4	.6	12
July 6	7.4- 9.6	8.2	.1	4

Hind Limb Length (mm)

June 14	.5- 1.4	1.0	.3	21
18	.7- 2.1	1.5	.4	21
22	2.2- 4.2	2.8	.5	17
28	4.5- 7.4	6.0	1.2	12
July 6	21.8-33.7	26.6	5.2	4
12	23.6-34.5	30.4	2.8	12

APPENDIX I. (continued)

Interorbital Distance (mm)

Date	Range	Mean	Standard Deviation	Sample Size
May 28	.8- 1.8	1.3	.3	26
June 14	2.9- 4.8	4.1	.6	21
18	4.1- 5.8	5.0	.5	21
22	4.8- 6.1	5.5	.4	17
28	6.9- 8.7	7.6	.5	12
July 6	6.2- 7.9	7.1	.8	4
12	5.5- 6.8	6.0	.4	12

Internaral Distance (mm)

May 28	.7- 1.2	.9	.1	26
June 14	1.1- 2.4	2.0	.3	21
18	1.9- 2.5	2.3	.2	21
22	2.4- 3.0	2.6	.2	17
28	2.9- 3.2	3.0	.1	12
July 6	2.4- 2.6	2.5	.1	4
12	2.1- 2.6	2.4	.2	12

Wet Weight (mg)

May 28	17- 34	24	6	6
June 14	204- 705	421	84	21
18	329-1061	658	100	21
22	656-1310	993	136	11
28	1674-2603	2109	154	12
July 6	1732-2540	2296	307	4
12	1050-1691	1408	151	9

APPENDIX I. (continued)

Dry Weight (mg)

Date	Range	Mean	Standard Deviation	Sample Size
June 14	5- 28	17	7	18
18	8- 47	24	10	21
22	38- 75	56	13	11
28	120-152	140	17	3
July 6	171-259	223	38	4
12	122-238	188	33	9

Ash Weight (mg)

Date	Range	Mean	Standard Deviation	Sample Size
June 18	1- 10	5	3	21
22	5- 13	9	3	11
28	14- 27	18	4	12
July 6	29- 37	33	4	4
12	17- 28	23	3	9

APPENDIX II. WOOD POND

Total Length (mm)

Date		Range	Mean	Standard Deviation	Sample Size
June	17	33.0-42.4	37.7	2.7	9
	21	31.7-50.7	42.4	5.9	21
	26	42.8-52.7	49.6	3.1	11
July	1	47.7-59.0	54.1	3.8	9
	5	47.0-63.9	56.1	4.8	15
	9	43.7-47.7	45.4	2.0	3

Standard Length (mm)

June	17	15.6-18.1	16.9	.8	9
	21	12.9-21.1	18.4	2.3	21
	26	20.3-24.6	22.4	1.5	11
July	1	19.7-24.3	22.7	1.3	9
	5	19.5-24.8	21.9	1.2	15
	9	18.0-19.6	18.9	1.0	3

Tail Height (mm)

June	17	8.7-11.5	10.0	.9	9
	21	8.1-21.1	11.4	1.5	21
	26	12.0-15.5	13.2	1.2	11
July	1	12.0-14.8	13.6	1.0	9
	5	8.5-15.0	12.8	1.6	15

Body Width (mm)

June	17	9.3-11.0	10.2	.6	9
	21	7.6-13.1	11.1	1.6	21
	26	11.6-13.9	13.1	.6	11
July	1	11.7-14.3	13.3	.9	9
	5	10.3-14.0	12.6	1.3	15
	9	7.5- 9.3	8.5	1.0	3

APPENDIX II. (continued)

Body Depth (mm)

Date	Range	Mean	Standard Deviation	Sample Size
June 17	6.4- 8.0	7.2	.5	9
21	5.4- 9.4	8.1	1.0	21
26	8.4-10.7	9.5	.7	11
July 1	7.5-10.6	9.2	1.0	9
5	6.5-10.0	8.5	.9	15

Hind Limb Length (mm)

June 17	1.3- 1.9	1.7	.2	9
21	1.3- 3.3	2.4	.6	21
26	2.7- 6.3	5.1	1.1	11
July 1	4.6-18.0	10.1	4.2	9
5	5.2-25.0	16.5	5.3	15
9	22.9-25.1	24.0	1.1	3

Interorbital Distance (mm)

June 17	4.0- 5.9	4.9	.6	9
21	3.9- 6.7	5.7	.7	21
26	6.4- 7.5	6.9	.3	11
July 1	5.6- 7.3	6.8	.5	9
5	5.9- 7.5	6.8	.5	15
9	5.0- 6.0	5.4	.5	3

Internaral Distance (mm)

June 17	1.5-2.5	2.2	.3	9
21	2.1-2.9	2.5	.2	21
26	2.6-3.0	2.8	.1	11
July 1	2.4-2.9	2.7	.2	9
5	2.0-3.0	2.5	.3	15
9	2.0-2.2	2.1	.1	3

APPENDIX II. (continued)

Wet Weight (mg)

Date	Range	Mean	Standard Deviation	Sample Size
June 17	502- 894	735	138	7
21	291-1433	926	309	21
26	984-1763	1433	281	11
July 1	1020-1937	1703	301	9
5	1211-2170	1659	297	15
9	748-1132	896	207	3

Dry Weight (mg)

June 17	25- 52	39	8	7
21	14- 75	48	18	21
26	53-119	91	19	10
July 1	68-168	131	32	8
5	93-207	146	29	15
9	85-113	102	16	3

Ash Weight (mg)

June 17	1- 5	2	1	7
21	1-11	6	3	20
26	8-18	14	3	10
July 1	8-20	17	4	9
5	11-30	19	5	15
9	10-14	12	2	3